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U. S. DEPARTMENT OF AGRICULTURE.

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 221.

B. T. GALLOWAY, *Chief of Bureau.*

DIMORPHIC LEAVES OF COTTON AND ALLIED PLANTS IN RELATION TO HEREDITY.

BY

O. F. COOK,

Bionomist in Charge of Crop Acclimatization and Adaptation Investigations.

ISSUED NOVEMBER 22, 1911.

WASHINGTON:
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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., April 28, 1911.

Sir: I have the honor to transmit herewith a paper entitled "Dimorphic Leaves of Cotton and Allied Plants in Relation to Heredity," by Mr. O. F. Cook, Bionomist in Charge of Crop Acclimatization and Adaptation Investigations of this Bureau, and to recommend its publication as Bulletin No. 221 of the Bureau series.

Numerous agricultural applications of the facts of dimorphism have been described in Bulletin No. 198 of this Bureau, entitled "Dimorphic Branches in Tropical Crop Plants: Cotton, Coffee, Cacao, the Central American Rubber Tree, and the Banana." The present paper reports additional information regarding the dimorphic characters and variations of cotton and other plants and points out their relation to problems of heredity and breeding. It is believed that more definite knowledge of the characters and habits of growth of our cultivated plants will be of assistance in many lines of agricultural investigation.

Respectfully,

Wm. A. Taylor,
Acting Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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DIMORPHIC LEAVES OF COTTON AND ALLIED PLANTS IN RELATION TO HEREDITY.

INTRODUCTION.

Parallel series of variations in the forms of the leaves can be traced through numerous species of cotton and also in other genera of Malvaceæ, such as Hibiscus, Abelmoschus, and Ingenhousia. The parallel variations appear as characters of different cultivated varieties and are also represented by dimorphic specializations of leaf forms in different parts of the same plant.

Though this class of variations has received little attention hitherto, the facts are of interest in relation to general questions of heredity and to the practical problems of breeding superior varieties and maintaining their uniformity by selection. Recognition of dimorphism of the leaves and branches in cotton and related plants enlarges the range of characters that may be used in distinguishing varieties and in determining the influence of environment upon the expression of characters.

The cotton plant affords unusually good opportunities for the study of environmental modifications, but it is essential that the characters and habits of the various cultivated forms be well known if the differences of behavior in different conditions are to be correctly understood. Studies of environmental differences or of correlations of characters that do not take into account the normal diversity in the structure of the different parts of the plant may give very misleading results.

Though different kinds of leaves or branches represent very definite facts of heredity, yet the expression of such characters can be influenced by external conditions. Thus it has been found that new conditions may seriously disturb the expression of characters in the cotton plant, even to the extent of a complete suppression of the fruiting branches, so that the plants remain completely sterile, although showing a high degree of vegetative vigor. The behavior of such plants may be compared with that of sterile hybrids. In both cases there is a failure to bring the full series of normal characters into expression.[1]

[1] Cook, O. F. Dimorphic Branches in Tropical Crop Plants: Cotton, Coffee, Cacao, the Central American Rubber Tree, and the Banana. Bulletin 198, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1911, pp. 18–27.

For the purposes of the selection that has to be maintained in order to keep a superior stock in a condition of uniformity, it is quite as important to recognize varieties by the characters of their leaves and branches as by those of the bolls and seeds. Indeed, selection by vegetative characters can be made even more efficient than selection by fruit characters because it enables degenerate variations to be recognized and removed early in the season, thus avoiding the danger of spreading inferior characters through cross-pollination.[1]

Selection is our means of keeping undesirable characters from coming into expression, but it does not prevent the transmission of such characters. Even though all the lines of descent that show tendencies to the expression of undesirable characters be rejected, the possibilities of such expression remain in the other lines and are likely to be reawakened if selection be relaxed. One of the most important problems in the selective breeding of cotton and other seed-propagated field crops is to make selection more efficient by more adequate knowledge of the characteristics and behavior of the plants, so that deviations from a type can be more easily recognized and removed from the stock and the exciting causes of such deviations avoided.

DIMORPHISM A PHENOMENON OF ALTERNATIVE EXPRESSION.

The most important of the general facts or principles of heredity that may be illustrated by the phenomena of dimorphism is the fundamental distinction between expression and transmission. Unless this distinction is appreciated it is impossible to understand the measures of selective breeding that are required to preserve the uniformity and maintain the agricultural value of superior varieties of cotton and other seed-propagated crop plants. Many efforts are being made to solve the problem of heredity by seeking in the protoplasm of germ cells for microscopic organs or mechanisms that are supposed to transmit the characters from the parents to the offspring. While the discovery of such a mechanism would be of great scientific interest, the facts of heredity that promise to be of most value from the standpoint of agricultural application are facts of expression. Even without determining the mechanism of transmission it is possible to investigate the effects of breeding and environment upon the expression of characters.[2]

The doctrine elaborated by Weismann that there is a fundamental distinction between the germ plasm and the protoplasm of the somatic or vegetative tissues has doubtless tended to prolong the

[1] Cook, O. F. Cotton Selection on the Farm by the Characters of the Stalks, Leaves, and Bolls. Circular 66, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1911.

[2] Cook, O. F. Transmission Inheritance Distinct from Expression Inheritance. Science, n. s., vol. 25, 1907, p. 911.

confusion of the facts of expression with those of transmission. The phenomena of inheritance have been supposed to center exclusively in the germ cells, the assumption being that all the characters that are to be shown in the adult are determined beforehand in the germ cells. The facts of dimorphism suggest that the phenomena of heredity and breeding can be studied in the vegetative parts of the plants as well as in the floral or reproductive organs or in the protoplasmic mechanism of the germ cells.

The production of a succession of different kinds of internode individuals by vegetative propagation shows that characters may be brought into expression and then suppressed and replaced by other characters without the necessity of new conjugations to form new germ cells. In all the higher plants the expression of the characters is changed repeatedly during the growth of each individual. This may be one of the reasons why the processes of heredity appear to be more susceptible to environmental influences in plants than in animals.

That the leaves and other vegetative parts of many plants do not have the power of regenerating or bringing the characters of the other parts into expression does not demonstrate a fundamental difference between the germinal and somatic protoplasm. In some plants, such as the Begonia, it is evident that all of the tissues inherit all of the characters, since new plantlets are able to bud out freely from the leaf blades, petioles, and stalks.

In Bryophyllum also young plantlets are produced from the leaves, but only from particular points along the margins instead of from the whole surface of the leaf. But even with the most definite limitations of expression there may be evidences of complete transmission. Thus lateral branches of coffee, though apparently quite unable to produce upright shoots from vegetative buds, are certainly able to transmit all the characters of the species, for all the fruit is produced on the lateral branches.

If there were a complete correspondence between expression and transmission, so that the transmitted characters of a variety could be fully known from a single individual or from a generation of uniform individuals, the characters of a pure-bred uniform variety might be expected to remain fixed for all time and further selection would be entirely unnecessary, as assumed in some theories. But in reality no such permanent uniformity has been found to exist. No refinement of the breeder's art establishes an unchanging expression of characters in any seed-propagated plant, or even in those that are increased by vegetative propagation. It is easy to understand that selected strains of wheat or other plants adapted to self-fertilization may show greater and more permanent uniformity than

varieties of cross-fertilized plants like cotton and corn, but the idea of an absolutely fixed or constant expression of characters does not accord with the facts of biology.

The successive formation of the different organs of the plant represents a series of changes in the expression of the characters, often as definitely contrasted as differences between varieties or species. Even in purely vegetative organs like the leaves specialized dimorphic changes of expression may be established in some species, instead of more gradual or continuously varied changes that appear in related species or even in other varieties of the same species.

In the study of heredity, as in many other fields of scientific exploration, there is a tendency to give special values to evidence drawn from remote or difficult sources and to overlook the significance of familiar facts or of those that are capable of easy and direct observation. Yet it must be recognized that any underlying principles or general facts of heredity that are to be of practical use must have relation to readily visible external characteristics of our most familiar domestic animals and plants. The more familiar the facts, the more ready and reliable should be the interpretation, were it not for the greater interest generally secured by more remote and more doubtful considerations.

Though some of the facts described in this paper may not have been previously recorded in connection with the cotton plant and its relatives, similar facts are common enough in other genera and families of plants. The dimorphic leaves and branches of cotton and other related plants do not represent extreme types of specialization, but this may give them the greater interest from the standpoint of heredity because of the intermediate position between the more definite and less definite forms of alternative inheritance.

It is usual to think of plants as simple individuals, but in reality they are compound individuals built up by the association of many individual internodes or metamers, each of which may be capable of an independent existence. The internode individuals are not all of one kind. In addition to the specialization of some of them as floral organs definite differences are often to be found among the vegetative metamers. The fact that many plants seem to lack definite specializations among the vegetative internodes only renders such peculiarities the more interesting when they occur, for they throw another light on the facts of evolution and heredity.

The development of any individual plant may be viewed as a progressive change of expression of characters, the juvenile characters giving place to the adult, but the changes are generally so gradual as to suggest no analogy with the Mendelian form of definitely contrasted alternative inheritance. Abrupt changes from juvenile to

adult forms of foliage have long been known in such cases as junipers and eucalypts, but these have not been considered as of the same nature as the contrasted inheritance of Mendelian characters. In the case of the cotton and Hibiscus, however, it appears that Mendelian relations exist in characters that are also subject to abrupt change during individual development. Mendelian inheritance is associated with other contrasted changes in the expression of characters. The same characters that show contrasted expression in Mendelian hybrids may be as definitely contrasted, in related plants, in the growth of each individual. Mendelism, like the dimorphic differences, may be looked upon as representing alternative expression of characters instead of alternative transmission.

ABRUPT CHANGES OF LEAF FORMS IN HIBISCUS CANNABINUS.

A very pronounced example of dimorphism of leaves was observed in Egypt, in May and June, 1910, in *Hibiscus cannabinus*, the so-called Deccan or Ambari hemp, a plant commonly grown along the borders of cotton fields. The object of planting the hemp with the cotton is to avoid the injuries of the plant lice, which are usually severe on the more exposed margins of the fields. Though the hemp plant is a rather close relative of the cotton, it is much less susceptible to the attacks of the insects and grows up more rapidly. The cotton field is protected against the drier outside air that might otherwise enable the plant lice to destroy the outer rows. Moreover, a bast fiber extracted from the Hibiscus is made into a coarse cordage used for many agricultural and domestic purposes.

Variations of leaf forms in the hemp plant show a curious parallel with cotton. In addition to the entire or very broadly lobed leaves comparable to those of ordinary Upland varieties of cotton, there are other varieties with deeply divided narrow leaves, like the so-called "okra" varieties of cotton in the United States, and some with leaves parted to the base into narrow digitate segments, a condition also known in some of the tropical varieties of cotton. (Pls. I, II, and V.)

Further similarity was found in the fact that the Egyptian variety of *Hibiscus cannabinus* with the lobed leaves produced entire leaves at the base of the stalk, as also happens with the narrow-lobed "okra" varieties of Upland cotton. The Hibiscus leaves show a very abrupt transition from the broad, simple form of leaves on the lower part of the stalk to the narrow, deeply lobed form on the upper part (fig. 1); this abrupt change in the characters of the leaves seemed the more worthy of notice on account of the fact that Mendelian segregation of the broad and narrow forms of leaves has been found to occur in the second generation of crosses between

varieties of cotton representing two corresponding types of leaves. The hemp plants with the two kinds of leaves represent a segregation of characters among the internode members of the same plant.

The leaves of the upper part of the stem are all deeply lobed, while those of the lower part are without lobes. The transition is usually quite abrupt, though the leaves that are close to the transition are often slightly different from others of the same class. A premonition of the change may be found in the larger marginal teeth of the last of the undivided leaves (fig. 2), or the last simple leaf may have a prominent angle on one or both sides (fig. 3). A more definitely intermediate condition appears when a leaf is divided on one side

FIG. 1.—Growing tips of stalks of *Hibiscus cannabinus*, showing changes from simple to lobed leaves. (Natural size.)

but not on the other. (See Pl. II.) In such cases there is usually a very pronounced difference between the two sides of the leaf, so that the change from the entire to the lobed condition is still quite abrupt in comparison with the very gradual changes shown in many plants in passing from the large basal or radical leaves to those of the upper part of the stalk.

Specimens to illustrate the abrupt nature of the transition from the entire to the lobed form of leaf (Pl. I) were taken quite at random, except for the necessity of seeking plants that had uninjured leaves at the nodes where the transition took place. Many of

the leaves were badly mutilated by the bites of insects. It was also necessary to search a little farther to find examples of more gradual transition from the entire to the divided state. (See Pl. II.)

Those who prefer mathematical statements of such facts might measure the depths of the incisions of the leaves and construct curves or other numerical expressions of the differences of form, but the nature of the differences is apparent in the photographic reproductions. It is evident from the abrupt ness of the transition that curves representing measurements of the divisions of the leaves would show two very distinct and well-separated modes, quite as distinct as those that would represent the expression of contrasted characters in cases of Mendelian segregation in the second generation of a hybrid.

FIG. 2.—Four leaves from successive internodes of the same stalk of *Hibiscus cannabinus*, showing slight differences among the simple leaves and abrupt change to the divided form. (Natural size.)

It is difficult to imagine that any practical advantage can be secured by the plants by changing the form of the leaves thus abruptly part way up the stalk. Yet it is possible that the different forms of the leaves may be connected with the fact that there is a difference of function among the internodes of the stalk. The internodes of the upper part of the stalk produce fruit or fruiting branches, while those of the lower part do not. Some of the lower internodes of the cotton stalk give rise to large vegetative limbs with the same functions as the stalk, while other internodes produce only small abortive branches or none at all. Several of the barren internodes usually intervene between the highest of the vegetative limbs and the lowest of the functional fruiting branches, as though it were difficult to change abruptly from one form of branches to the other.

In Deccan hemp and the okra plant the fruits are borne directly at the axils of the main stalk without the intervention of fruiting branches. It may be that the divided leaves indicate in advance the internodes that are to produce flowers and fruit. Change of leaf form marks the approach of the fruiting condition in such plants as *Hedera helix* and *Ficus repens,* but in such cases the change of leaf forms does not occur on the same axis of growth. The creeping stems of the juvenile stage represent an adaptive condition inter-

calated into the life histories of these plants, like the larval stages of insects.

The joints of the stalk of the cotton plant may also be considered as dimorphic with reference to the two kinds of branches that they produce, but it is a further step in hereditary specialization if the joints prove to be differentiated also by the forms of leaves that subtend the two kinds of branches. The external conditions often appear to influence the number of vegetative branches, but it is not yet known whether such changes are caused by direct transformations in buds already formed or are previously determined in the growth of the primary stalk. It may be that differences in the forms of the leaves will help to show when the characters of the branches are determined.

FIG. 3.—Leaves from adjacent internodes of *Hibiscus cannabinus*, showing transition from the simple to the divided form, but with the lobes indicated in the simple leaf by prominent angles. (Natural size.)

In Upland varieties of cotton the fruiting branches are produced closer to the base of the plant than in the Egyptian cotton, and the seedlings of Upland cotton also begin to produce lobed leaves at earlier stages than Egyptian seedlings. The second or third leaves of Upland cotton often show distinct lobes, and in some varieties, such as "Willet's Red Leaf," even the first leaf may be lobed. In the Egyptian cotton, where the vegetative branches are more numerous and the fruiting branches begin farther up the stalk, the seedlings usually produce from five to seven entire leaves before the lobed leaves begin to appear. In luxuriant plants the vegetative branches continue farther up the stalk than the entire leaves, but under other conditions the vegetative branches are less numerous. Fruiting branches have

been found on the Egyptian cotton in Arizona as low as the seventh node, as reported by Mr. Argyle McLachlan.

LEAF FORMS OF VARIETIES OF HIBISCUS CANNABINUS.

At least two varieties of the Deccan hemp are grown in Egypt, one with deeply divided, finely toothed leaves (Pls. I and II) and the other with more coarsely toothed, undivided leaves (figs. 1, 2, 3, and 4). It does not appear that either of these Egyptian varieties has been introduced into the United States, but a third variety with digitately parted leaf blades, not seen in Egypt but supposed to come from India, has been grown experimentally in Louisiana. (Figs. 5 and 6.)

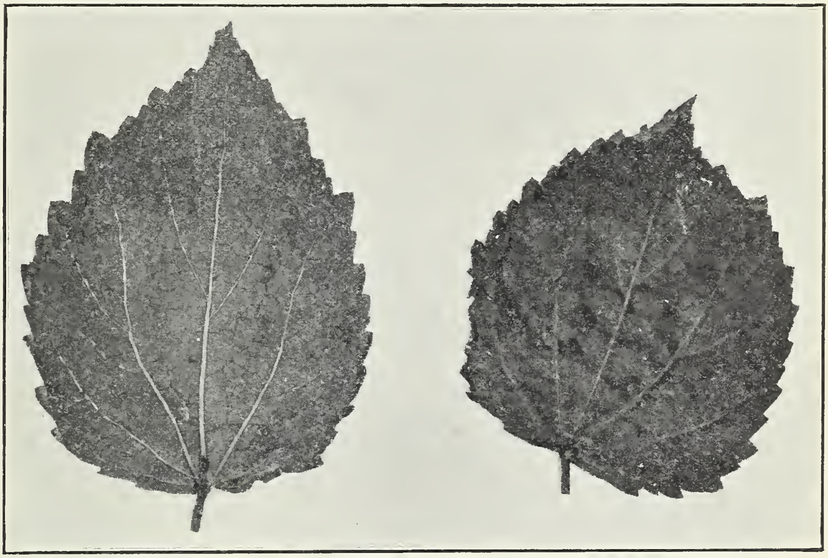

Fig. 4.—Simple-leaved Egyptian variety of *Hibiscus cannabinus*. (Natural size.)

The variety with the dimorphic leaves is much more generally planted in Egypt, but plants with broader, undivided leaves are often found growing with the others. At Tanta, to the north of Cairo, separate plantings of the broad-leaved variety were seen. The plants seemed larger, coarser, and of a darker green color than those of the narrow-leaved type growing in the same locality. The leaves are distinctly larger and with the margins much more coarsely toothed. A tendency to the lobed form of leaf seemed to be indicated in this variety only by the somewhat larger teeth at the ends of the largest of the oblique veins. There may be a general correlation between the shape of the leaf and the size of the marginal teeth. The teeth seem to be larger in the undivided leaves of the

dimorphic variety than in the lobed leaves. The smallest teeth are found on the specimens with the very narrow digitate lobes. (See figs. 5 and 6.)

Examples of transition forms of leaves seem to be more common on plants with rather small, narrow-pointed, sharply dentate leaves than in plants with larger leaves and less numerous teeth. (See Pl. II, *A*, *B*, *C*, and *D*.) It is not impossible that these differences represent distinct varieties or strains. There is no reason to suppose that the Egyptian varieties of this plant have been subjected to any more close or careful selection than the Egyptian varieties of cotton, which were found to exhibit a wide range of diversity.

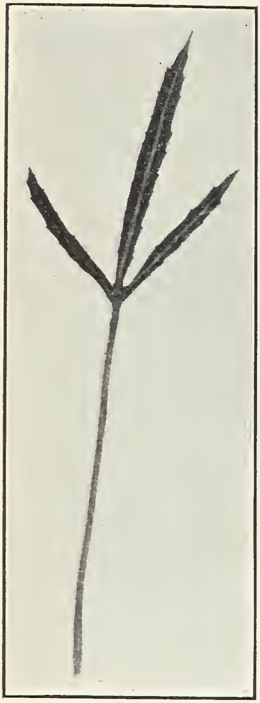

Fig. 5.—Three-lobed leaf of narrow-lobed variety of *Hibiscus cannabinus*, grown in Louisiana. (Natural size.)

In Hooker's "Flora of British India" the leaves of *Hibiscus cannabinus* are described in two slightly different ways, once "Lower leaves entire, upper lobed," and again "Lower leaves cordate, upper deeply palmately lobed, lobes narrow serrate." The narrow-lobed variety shown in figures 5 and 6 would seem to conform most nearly to this description, though none of the lower leaves are shown in the pressed specimens of this variety in the Economic Herbarium of the United States Department of Agriculture. The species seems not to be represented in the National Herbarium. The leaves of the Egyptian varieties would hardly be described as cordate, though some of those in Plate II show a slight reentrant angle at the base.

The lobing of the leaves of the dimorphic Egyptian variety is not unlike that of the plant depicted as *Hibiscus cannabinus* in Roxburgh's "Plants of the Coast of Coromandel" (vol. 2, pl. 190), except that some of the upper leaves are shown with five lobes. Though no such leaves were seen on the Egyptian plants in July it is quite possible that they occur later in the season. Roxburgh also gives a separate figure of a simple narrowly lanceolate leaf and states that this form occurs at the top of the full-grown plants. According to Wester a similar reduction of the later leaves is shown in the roselle plant (*Hibiscus sabdariffa*).[1]

[1] Wester, P. J. Roselle: Its Culture and Uses. Farmers' Bulletin 307, U. S. Dept. of Agriculture, 1907, p. 7. "The leaves on the young plants are entire; as the plant increases in size the leaves change to palmately five parted; later the leaves in whose axils the flowers are borne are three parted."

PARALLEL LEAF FORMS IN COTTON.

The dimorphism of the leaves of *Hibiscus cannabinus* is the more interesting because a closely parallel series of leaf forms appears in the cotton plant. Entire or broad-lobed leaves are found in all varieties of cotton, at least during the early stages of growth, the lobes becoming more pronounced with maturity. (Figs. 7 and 8.) Narrow-leaved varieties of Upland cotton, popularly known as "okra" cotton, show a dimorphism corresponding quite closely to that of the dimorphic-leaved Egyptian variety (fig. 9), and others have a still more deeply divided, strongly digitate form, like the variety of *Hibiscus cannabinus* grown in Louisiana (fig. 10). Young plants of okra cotton have, at first, entire or broad-lobed leaves like the seedlings of other varieties of Upland cotton, but whether the change is gradual or abrupt has not been noticed.

FIG. 6.—Five-lobed leaf of narrow-lobed variety of *Hibiscus cannabinus*, grown in Louisiana. (Natural size.)

Individual plants with narrow-lobed leaves appear occasionally as mutative variations in broad-lobed varieties. Thus the narrow-lobed leaf shown in figure 9 represents a variety called "Park's Own," said to have originated as a variation of the King variety. (See fig. 8.) Several other mutations have been observed in experimental plantings of the King cotton in Texas showing different degrees of expression of the tendency to narrow lobes.

Transitions from entire to broadly lobed leaves are to be found on nearly every plant of Upland cotton, though entire leaves are more abundant on some varieties. Vegetative branches often have small, entire leaves, like those of young seedlings, on the short basal internodes. The proportion of entire leaves also seems to differ in varieties and is influenced by conditions of growth, humid greenhouse conditions having a distinct tendency to produce more of the entire leaves and to reduce the lobes of the others.

An individual plant of Triumph cotton found in a field at San Antonio, Tex., in September, 1910, showed a marked variation

toward the simple form of leaves. The seed, unfortunately, had all been picked, so that the inheritance of the variation could not be tested. The plant appeared unusually vigorous, but had the advantage of standing at the end of the row. Most of the leaves were simple and entire (fig. 11), only a few being three lobed and these with the lobes unusually short. A count showed 152 simple leaves and 41 with lobes. Some of the wild species of cotton have all the

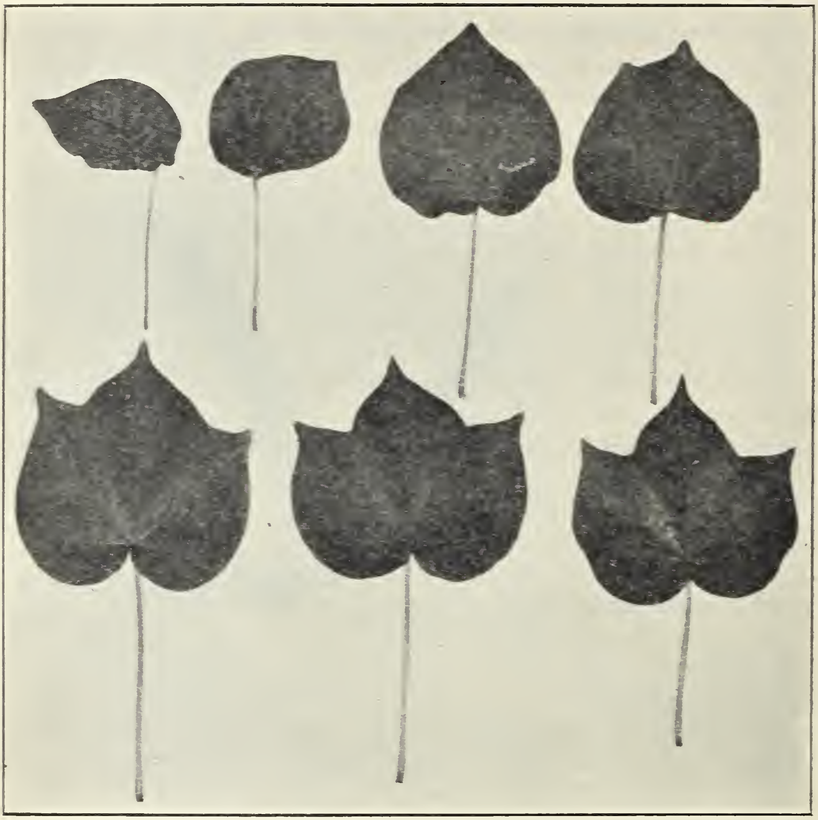

Fig. 7.—Leaves of Upland cotton seedling from first seven nodes above the cotyledons, showing changes of form. (Natural size.)

leaves simple, and thus complete the correspondence with the simple-leaved Egyptian variety of *Hibiscus cannabinus*.

The tendency to reduction of the lobes under greenhouse conditions represents another phase of the general parallelism of leaf forms. This tendency seems to be very general, not only in different varieties of Upland cotton, but also in the Egyptian and Sea Island types that in open-air conditions have the lobes more highly developed than those of Upland cotton. The fruiting branches of green-

house plants of Egyptian cotton have many of the leaves of the fruiting branches quite simple, a character that appears very seldom in open-air plants. A comparison of figure 12 with figure 14 will give an idea of the range of variation in leaf forms on the fruiting branches of the Egyptian cotton and of the extent to which the expression of the characters may be modified by external conditions. It may also be noted that the entire leaf of the Egyptian cotton grown under greenhouse conditions is broader and less pointed than that of the Upland cotton grown in Texas under open-air conditions. As the figure also shows, the texture of the entire Egyptian leaf is much more delicate than that of the Upland leaf, which is not true in outdoor plants of Egyptian cotton.

The greater tendency of the Egyptian cotton to produce entire leaves is also apparent in the early stages of growth. Lobed leaves develop on young plants of Upland cotton from lower joints than in Egyptian cotton, as already noted. Hybrids between Upland and Egyptian cotton, grown at Bard, Cal., in 1911, were intermediate in this respect and usually began to show lobed leaves on the third joint above the cotyledons. The transition from the entire to the lobed form of leaves was much more gradual among the hybrids than in pure Egyptian plants. Very large luxuriant seedlings of the Egyptian cotton, with vegetative branches already pushing from the nodes of the cotyledons, seemed to show less definite transitions in leaf form than the somewhat smaller and more normal plants where the buds in the axils of the cotyledons had remained dormant. Failure of the normal specialization of leaf forms would correspond with abnormalities in the formation of the branches that occur very frequently in the Egyptian cotton under conditions of too luxuriant growth.

FIG. 8.—Mature leaf of "King" Upland cotton, parent of "okra-leaved" variations. (Natural size.)

TWO TYPES OF DIMORPHISM OF LEAVES IN COTTON.

The dimorphism of leaves in Hibiscus is of the same type as that of the narrow-leaved "okra" cottons, as already indicated. But there is another type of dimorphism of leaves in cotton, connected with a definite dimorphism of the branches. The leaves of the fruiting branches of cotton are smaller than those of the main stalk and vegetative branches and often have nectaries on only one or two of

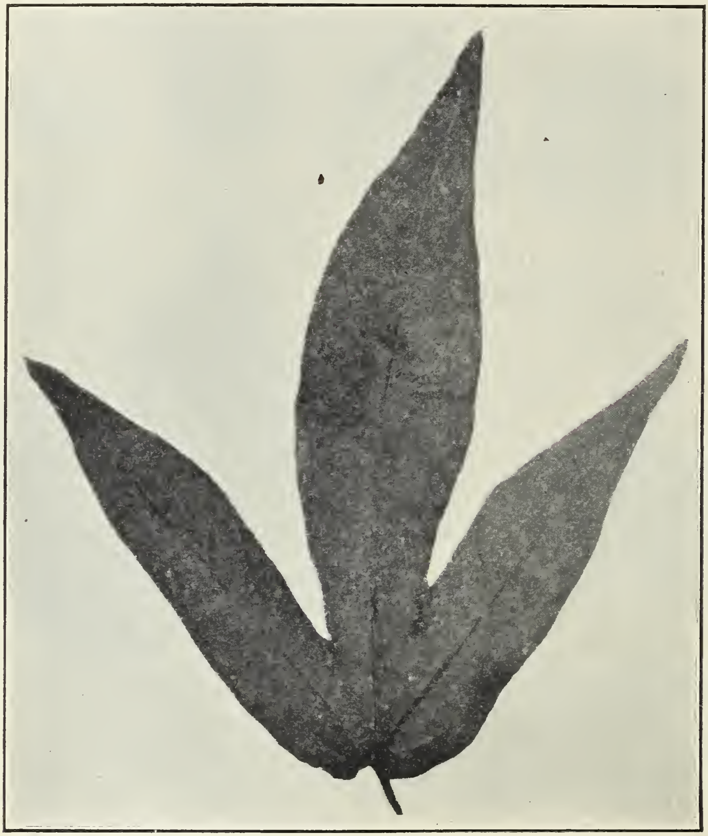

FIG. 9.—Leaf of "Park's Own," an "okra" variety of American Upland cotton. (Natural size.)

the principal veins, even when the leaves of the main stalk and vegetative branches have three nectaries with much regularity.

The dimorphism is not so easily recognized in the blades of the leaves, because of the general freedom of variation in sizes and shapes, but appears much more definite when attention is given to the stipules. On the main stalk and the vegetative branches the leaves have the two stipules equal in size and narrowly lanceolate or strap

shaped (fig. 13), while on the fertile branches of the same plant one stipule may be much broader than the other (fig. 14). Broadening of one of the stipules is a usual and apparently quite normal characteristic of the Egyptian cotton. (Pl. III.) It also appears in a related African type from the Niam Niam, in the upper valley of the White Nile. On the other hand, the enlargement of the stipules and the corresponding reduction of the petiole and blade of the leaf sometimes represents a distinctly abnormal tendency, accompanied by frequent abortion of the flower buds. In such cases the leaves of the fruiting branches become reduced and more or less intermediate in form between the normal leaves of the fertile branches and the involucral bracts that inclose the flower buds. (Pl. IV.)

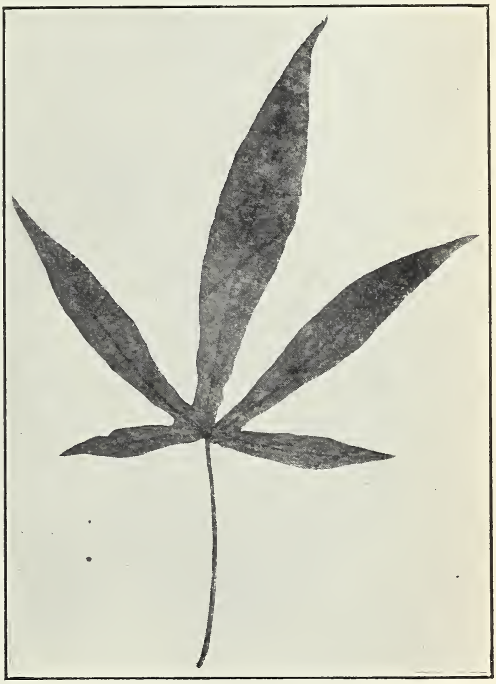

Fig. 10.—Leaf of "Ratteree's Favorite," an "okra" variety of American Upland Cotton. (Reduced.)

These abnormal intermediate forms of leaves illustrate the nature of the transformation that has taken place in the specialization of the involucre of the cotton plant. Each of the three bracts that compose the external involucre represents a leaf with the blade much reduced, the petiole entirely suppressed, and the stipules greatly enlarged and united with the blade. In the abnormal intermediate forms of leaves a reduction of the petiole and blade is usually accompanied by a corresponding increase of the stipules, though one is generally much larger than the other. (Fig. 15.)

In contrast with the other leaves of the plant, the bracts might be considered as an extreme case of dimorphism, since the differences of form are much greater than those of the different types of foliage leaves. The occurrence of the intermediate forms between bracts and foliage leaves is also quite rare. Under some conditions of growth such intermediate forms seldom or never occur, but under other conditions, or at the end of the season, the normal specializations of

inheritance seem to relax and the abnormal intermediate forms begin to appear. They are much more common in the Egyptian cotton than in the Upland and have shown themselves most frequently in a peculiar fastigiate variety of the Egyptian cotton introduced into Arizona under the name of "Dale," perhaps the same as the variety called "Bamieh" in Egypt.

Other series of abnormalities serve to connect the outer involucre of the cotton flower with the inner involucre, or so-called calyx, as though

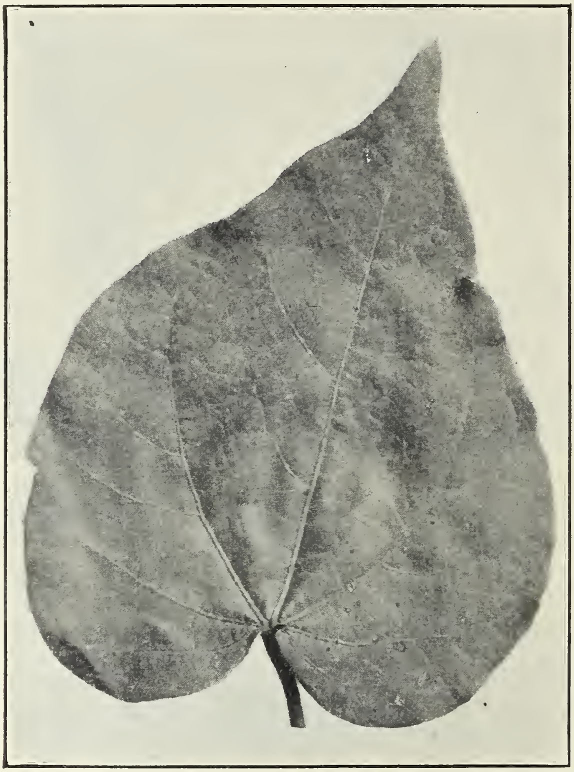

FIG. 11.—Cotton leaf without lobes, a variation of the Triumph variety. (Natural size.)

this organ were formed from another type of reduced and specialized leaves. The petals, on the contrary, seem to represent specialized stamens rather than specialized leaves. They are inserted on the base of the staminal column. Their development from stamens is also suggested by the small, expanded, petal-like organs that are sometimes found on the staminal column above the true petals. In such a case the petals or the stamens might be said to be dimorphic, or it might be considered that there has been a failure of the normally complete change in the expression of the characters in passing from the petals to the stamens.

PARALLEL LEAF FORMS IN OKRA.

The similarities of variations of leaf form in cotton and Deccan hemp do not exhaust the series of parallelisms. The okra plant (*Abelmoschus esculentus*) also shows the same general range of forms of leaves. Some varieties have broad leaves with very short, rounded

FIG. 12.—Simple leaf of fruiting branch of Egyptian cotton, produced under greenhouse conditions. (Natural size.)

lobes; others have rather narrow lobes, separated to below the middle, and there is a third type with very narrow segments digitately divided to the base. Though attention has not been paid to the

nature of the transition from broad to narrow leaves, it is probable that varieties differ considerably in this respect, for Mr. W. R. Beattie informs the writer that broad-leaved varieties will sometimes show a few deeply divided leaves late in the season. Two general types of pods are recognized, but there seems to be no very definite relation between the form of the leaf and that of the pods. Long, narrow pods are not confined to narrow-leaved varieties, but

FIG. 13.—Young leaf from vegetative branch of Egyptian cotton, with five lobes and equal stipules. (Natural size.)

are shared by broad-leaved sorts. Broad-leaved varieties seem to produce the thickest pods, but some of the narrow-leaved sorts have short pods.[1]

The prevalence of the broad-leaved forms of okra in Egypt is doubtless the explanation of the fact that the name Bamieh or

[1] Beattie, W. R. Okra: Its Culture and Uses. Farmers' Bulletin 232, U. S. Dept. of Agriculture, 1905. pp. 12–16.

"okra" cotton is given in Egypt to a variety having unusually broad and heavy leaves, the direct opposite of the variation to narrow-lobed leaves that characterizes the so-called "okra" cottons of the United States. The occurrence of broad-leaved varieties in Egyptian cotton corresponds to the narrow-leaved variations in Upland cotton. The normal foliage of the Egyptian cotton is of the same general form as some of the narrow-leaved or "okra" variations of the Upland type of cotton.

There is a popular idea in Egypt that the Bamieh or broad-leaved type of Egyptian cotton originated from natural crossing of cotton with okra, the same explanation that is given for narrow-leaved variations of Upland cotton in America. The Egyptian Bamieh cotton also produces all of its bolls close to the main stalk, like the okra plant. American Upland varieties of the "okra" type do not have this short-branched habit.

FIG. 14.—Young leaf from fruiting branch of Egyptian cotton, with three lobes and unequal stipules. (Natural size.)

The parallelism of leaf characters between cotton and okra extends even to the presence of a distinct red spot at the base of the leaf at the junction with the petiole. The presence of such a spot on the leaves of a cotton plant is reckoned in Egypt as a distinctive character of the inferior Hindi type that is responsible for a serious deterioration of the Egyptian stock. The leaves of the Hindi cotton are also a distinctly lighter shade of green than those of the Egyptian cotton, matching the color of the okra leaves very closely. These similarities are doubtless responsible for another popular theory, that the Hindi contamination of the Egyptian cotton is due to crossing with the okra plant.

The presence of the red basal spot in the okra and other relatives of cotton is of interest from the standpoint of heredity, in view of the fact that this character shows a somewhat contrasted or Mendeloid expression in hybrids of Egyptian with Hindi or Upland varieties. The contrasting variations of color are not confined to the hybrids, but may appear in the different stages of the same plant.[1]

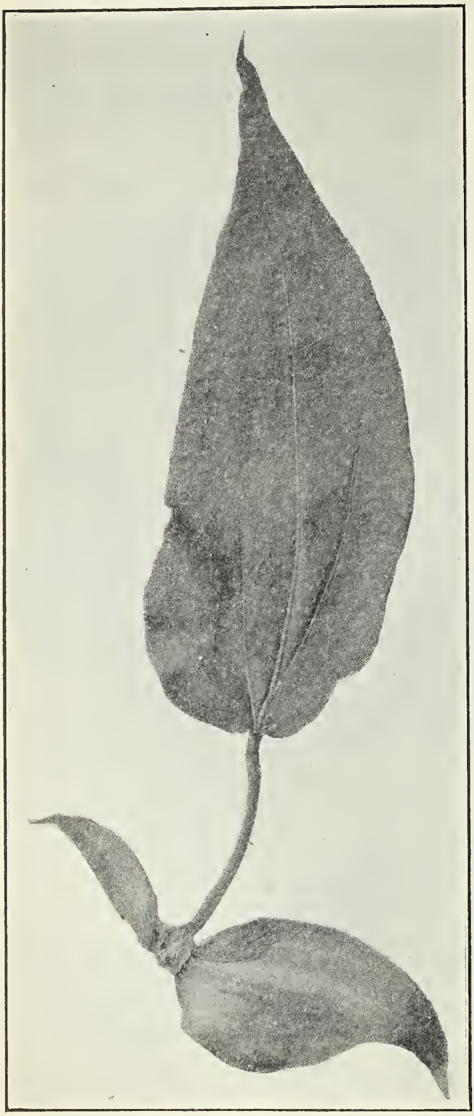

Fig. 15.—Leaf of fruiting branch of Egyptian cotton, with abnormally reduced blade and enlarged, bractlike stipule. (Natural size.)

Varieties of okra with the intermediate or narrow-lobed leaves seem to be most common in the United States, but in Egypt, where this crop is much more important than with us, broad-leaved varieties are grown almost exclusively. Okra, as well as *Hibiscus cannabinus*, is commonly planted with cotton in Egypt; but usually to take the place of hills of cotton that have failed to grow, instead of being confined to the borders of the fields.

The only narrow-lobed okra plants noticed in Egypt were a few near Medinet, in the Fayum Oasis. Very little of this variety was said to be planted. The fruits are considered more delicate, but are smaller than those of the broad-leaved plants. In the narrow-lobed variety there was an abrupt change from the broad-lobed leaves of the lower part of the stem to the adult form of leaves, but even the broad-lobed leaves were more deeply divided than those of

[1] Cook, O. F. Mutative Reversions in Cotton. Circular 53, Bureau of Plant Industry, U. S. Dept. of Agriculture, March, 1910, p. 10.

a broad-lobed variety included in the same planting. In the latter the lower leaves were almost entire, as often occurs in broad-lobed types of cotton.

SIGNIFICANCE OF PARALLELISM IN THE STUDY OF HEREDITY.

The parallel series of leaf forms of cotton and related plants are of interest in connection with many problems of heredity and breeding. In view of the fact that the same wide range of diversity in leaf forms exists in Gossypium, Hibiscus, and Abelmoschus, it becomes easier to look upon such differences as within the usual range of variation for this group of plants. Changes of characters to wider or narrower leaves do not require us to believe that a new character has originated or that hybridization with a different type of cotton has occurred.

The theory of hybridization as a cause of diversity of leaf forms is rendered the more unnecessary because the wide range of leaf differences appears not only in the same species or variety, but on the same individual plant. This is well shown in a wild relative of cotton, *Ingenhousia triloba*, native in Arizona. (Fig. 16.) The young plants have entire and broad-lobed leaves, while the leaves of adult plants have long narrow lobes. The branches of Ingenhousia, grown under greenhouse conditions, do not show the same tendency as in cotton to return to simple leaves, but the three-lobed leaves at the base of the branches have very short and broad lobes, quite unlike the tapering long-pointed lobes of subsequent leaves of the same shoot. The upper leaves have five lobes, as in cotton, okra, and *Hibiscus cannabinus*.

Fig. 16.—Plant of *Ingenhousia triloba*, showing transition from entire to deeply divided leaves. (Reduced.)

The fact that a wide variation in leaf forms occurs on the same individual plants in primitive wild species makes it entirely unneces-

sary to resort to the idea that variations in such characters in cultivated stocks must be due to previous hybridization. Some writers consider that uniform expression of characters, as in a carefully selected line-bred variety, represent the normal condition of heredity, and assume that this condition is found in wild species. The diversities that appear through variation are ascribed to hybridization, to the disturbing influence of the environment, or to mutative transformation into new species. Yet diversity is always found among the members of wild species as soon as the observer gains sufficient familiarity. The uniformity found in "pure-bred" varieties is an artificial product established and maintained by selection. The inferior variations that appear in selected strains of Upland cotton show the same range of diversity that is found among the members of primitive, unselected stocks. Such variations may reasonably be considered as reversions.

The return of latent characters to expression should not be looked upon as rare or exceptional, but as a normal phenomenon of heredity. Uniform expression of characters is rare and exceptional because the tendency to reversion is so general and persistent. Transmission is permanent, not variable like expression. Characters that have been suppressed for thousands of generations, like the incisor teeth of cattle, continue to be transmitted. Students of embryology recognize permanence of transmission by the law of recapitulation. The development of the embryo of a higher animal does not take a straight course from the egg toward the adult form, but remains closely parallel with the courses followed in lower groups. Many primitive characters are brought into slight or temporary expression, though they may disappear entirely before even the embryonic development is complete.

In view of the continued transmission of primitive characters, the tendency of the diversities of the wild types of cotton and other plants to reappear in selected varieties is more easily understood. In a diverse, unselected type each individual inherits and transmits from its many ancestors a large number of characters that are not expressed in its own body, and this transmission of latent characters continues even in the most carefully selected variety. Though opposed by selection, the natural tendency to alternation in expression also continues and becomes effective in the occasional individuals that show mutative variations.

It is true that examples of mutative reversion are usually not frequent enough to affect statistical investigations of other forms of expression of characters, but they are of essential importance in many questions of heredity and breeding. If the possibility of reversion and suppression of characters be left out of account, every definite

change of characters must be considered as the production of a new elementary species.

Mutative departures of occasional individuals from the characters of the parent stock are not uncommon in cotton, and differences in the forms of the leaves are one of the most readily distinguishable types of variation. Most of the variations that produce small bolls can be recognized in advance by their smaller and narrower leaves, or by other differences of vegetative characters.[1]

RELATION OF PARALLELISM TO CLASSIFICATION.

The importance of recognizing the fact of a general parallelism of variation in leaf form running through the different types of cotton and related plants is shown also in the field of classification. The genus Gossypium contains a large number of locally different forms of cultivated cotton, as well as numerous wild types. The classification of these into species and varieties is a difficult task of systematic botany. Failure to recognize the parallelism of variations has allowed the possession of narrow leaves to be taken as a sufficient proof of relationship. Narrow-leaved forms that are probably quite unrelated have been associated in the same species, while broad and narrow leaved forms of the same type of cotton have been treated as distinct species. These difficulties are well illustrated in a most elaborate monograph on the classification of cotton by Sir George Watt. The okra-leaved variations of American Upland cotton are repeatedly referred to in this work and add not a little to the complexities of the system of classification. Indeed, they are treated quite differently in different parts of the book and are even assigned to different botanical species.

The first suggestion is that the American okra-leaved forms represent a variety of an Asiatic species, *Gossypium arboreum*. This variety is alleged to have been introduced into North America at an early date and afterwards discarded from cultivation, as the following statements will show:

It was not until well into the seventeenth century that we possessed any trustworthy evidence of the Asiatic cottons having been carried to the New World. The Levant cotton (*G. herbaceum*) was the first to be taken to the United States and grown in Virginia. The Indian cottons (*G. obtusifolium*, various races) were conveyed to the States by the East India Co., and the Chinese and Siamese cotton (*G. nanking*) was carried by the French colonists to Louisiana about 1758. *G. arboreum* proper does not seem to have been successfully acclimatized anywhere in the New World, though the most important Asiatic (? hybrid) form derived from that species (*G. arboreum* var. *neglecta*) was early carried to America and the West Indies by the East India Co., and is known in the United States to-day under the name of "Okra" cotton.

There can thus be no doubt that Indian cottons were at an early date introduced into the West Indies and into the United States of America as well, and therefore

[1] Cook, O. F. Cotton Selection on the Farm by the Characters of the Stalks, Leaves, and Bolls. Circular 66, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1910.

very possibly this particular form, as also the far-famed Dacca cotton, stands every chance to have been carefully investigated in the New World. But the fact that *G. arboreum* var. *neglecta* has preserved in the United States, during probably close on 300 years of cultivation, identical characteristics to those it possesses under the widely different environment of India, argues strongly against the structural peculiarities by which it is recognized being viewed as merely geographical and climatological features, that change or disappear under altered conditions. * * *

But with reference to the survival of this presumably Indian plant in America and elsewhere (after its cultivation had been abandoned), it may be observed that once a particular species or race of cotton had been introduced into a favorable cotton-growing country, even though its regular cultivation might chance to be discontinued, it would be no great stretch of imagination to believe that a specially hardy stock, such as the present plant, might survive for centuries. * * * The fact, however, remains that *G. arboreum* var. *neglecta* has been repeatedly recorded as met with in the United States of America, and in the examples seen by me the plants in question could not possibly be separated botanically from the corresponding Indian stocks.[1]

It has not been found possible to produce hybrids between our American Upland varieties and the Asiatic species, though large numbers of experiments have been made in both India and the United States. In view of the failure to produce hybrids the Asiatic cottons can not be considered as close relatives of the American Upland type, though they show the same general range of variations of leaf forms. That the close similarity of leaf form should have led Watt to refer an American Upland cotton to an Asiatic species may be considered as a further testimony to the complete parallelism of variation.

Another okra-leaved variation of Upland cotton was considered by Watt to represent a hybrid of *Gossypium punctatum* or *G. hirsutum* and *G. schottii*, the last being a new species described by Watt as a wild plant in Yucatan. The idea that the narrow-leaved condition could be reached as a ''natural sport'' or mutative variation from a broad-leaved variety like the King is tacitly rejected in the following paragraph:

G. schottii, as defined by me above, must of necessity be a wild plant, since its inferior grade and low yield of wool would never justify its cultivation. It, however, matches sufficiently closely a hybrid found in a field of King's Improved cotton at Richmond, Va. (recently sent to me by Mr. Lyster H. Dewey of the Bureau of Plant Industry in the United States of America), as to countenance the belief that the so-called sport in question may have originated through the hybridization of *G. punctatum* or of *G. hirsutum* with the present species. The specimen came to me under the vernacular name of *okra*—a name that it will be recollected had on a former occasion been given to an American sample of *G. arboreum* var. *neglecta*. It is suggestive of the West Indian name *ochro* (*Hibiscus esculentus*) and possibly thus denotes the deeply dissected condition of the leaves. From the remark on the attached label of the present specimen it may be inferred that the American authorities were induced to believe that, though widely different from King's Improved, it was per-

[1] Watt, G. The Wild and Cultivated Cotton Plants of the World, 1907, pp. 81, 101, and 102.

haps but a natural sport. "Thousands of plants were grown from the seed, and but very few reverted to the broad-leaf type." [1]

In a later paragraph of the discussion of *Gossypium schottii* still another interpretation of the okra-leaved variations is proposed:

The bulk of the Upland American stock of present-day cultivation might be described, and accurately so, as consisting of forms of *G. mexicanum*. We read that repeated fresh supplies of seed have been procured direct from Mexico. It would thus be no great stretch of imagination to assume the possibility of hybridization of the cultivated stock of Mexico with the Yucatan *G. schottii* or some other allied form. Hence it is quite probable that King's Improved may itself be a hybrid of this nature, the split-leaved plant which appeared as if a saltatory variation being a recessive manifestation of the *G. schottii* characteristics. It is equally possible, however, that the fresh seed, imported from Mexico, may have been mixed and that the split-leaved plant had survived in the States for some years (and even got hybridized there) before its presence was recognized, just as the "Hindi weed cotton" of Egypt is reproduced year after year. In fact it might be possible to be a cultivated state of *G. schottii* in which no hybridization existed whatever, a weed of not sufficient importance to attract attention, which, once mixed, the seeds could not very readily be picked out from the supply reserved for future sowings.

If the narrow-leaved variations were a result of recent importations from Mexico they might be expected to appear more frequently in the Texas big-boll type of cotton and other varieties that Watt assigns to *Gossypium mexicanum* than in the King and other eastern small-bolled varieties that Watt holds to be more related to *Gossypium punctatum* and *G. hirsutum*. In reality the okra-leaved variations seem to be confined to the King and other small-boll types. They are certainly very rare in the big-boll varieties, if they occur at all.

For American readers it is hardly necessary to add that the theory of the existence of *Gossypium schottii* or any other wild type in the cotton-growing districts of the United States is not known to have any warrant of fact. There is a wild cotton in southern Florida, perhaps the same as that which has been described from the West Indies as *Gossypium jamaicense*. A specimen recently received from Mr. T. Ralph Robinson, collected by Mrs. Robinson on Terraceia Island in the lower part of Tampa Bay, indicates that the wild cotton of Florida extends farther to the north than has been supposed hitherto. Yet it would be a mistake to assume that it represents a close relative of our cultivated Upland varieties. The petals are yellow and have purple spots like those of the Egyptian or Sea Island cottons, instead of the white, spotless petals of the Upland varieties.

As a further example of the extent to which parallelism of leaf form may confuse classification, mention may be made of a curious, small-bolled, narrow-leaved cotton found by Messrs. G. N. Collins and C. B. Doyle at Tuxtla Gutierrez in southern Mexico, under the vernacular

[1] Watt, G. Op. cit., p. 207.

name "Culluche." The species has not been definitely identified, but Mr. F. L. Lewton suggests that it may represent Todaro's *Gossypium microcarpum* variety *rufum*. The leaves of the Culluche cotton are extremely variable in form, and many of them are quite simple. But instead of being broadly cordate like the simple leaves of Upland or Egyptian cottons, the simple leaves of the Culluche cotton are fusiform or lanceolate, much like the abnormal leaves of the Egyptian cotton shown in Plate IV and text figure 15. One of the simple leaves of the Culluche cotton is shown in figure 17. Comparison of this with the illustrations of the Egpytian cotton previously mentioned will show how close a resemblance of leaf forms may arise in species of cotton that are widely different in other respects.

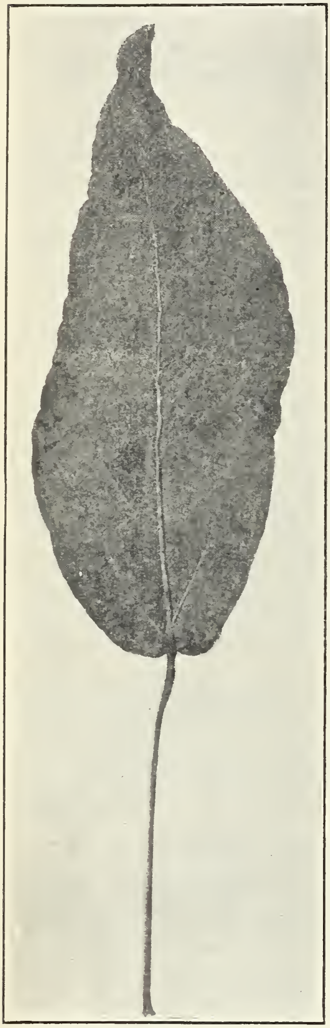

FIG. 17.—Simple leaf of Culluche cotton from Tuxtla Gutierrez, Mexico. (Natural size.)

RELATION OF DIMORPHISM TO MUTATION.

Viewed as a phenomenon of heredity, dimorphism of leaves presents an analogy with mutative variation. The fact that the abrupt change or contrast of characters occurs in the same individual plant instead of in separate plants should increase the interest attaching to such variations, especially if it appears that they are of the same general nature as the mutations that give rise to new varieties.

The change of characters involved in the production of dimorphic leaves has the most direct analogy with the rather rare phenomenon of bud mutation. Cases are known in which the expression of characters is changed in a single bud of a tree. A single branch of a tree shows a definite peculiarity not found in other branches or other trees of the same variety. A bud mutation of coffee seen in Guatemala some years ago had leaves as definitely unlike the remainder of the tree as any of the numerous seminal mutations of coffee that had been previously studied.

The most obvious difference between such a variation and the dimorphic branches and leaves of coffee, cotton, or cacao lies in the fact that the bud mutations are of rare and irregular occurrence, while the changes of characters shown in dimorphism are regularly repeated during the development of each individual plant or tree. The production of fertile branches in the cotton plant involves a mutative change of characters away from those that are expressed in the main stalk and the vegetative branches. But instead of producing normally only the one kind of branches with rare mutations to other kinds, the regular course of development for the cotton plant involves the production of two forms of branches, the vegetative form near the base and the fertile form farther up the stalk. In the Triumph variety of Upland cotton there may be said to be a double dimorphism, resulting in three forms of branches. The internodes of the lower fruiting branches are very short, like those of the branches of "cluster" varieties, though branches with internodes of normal length are produced farther up.

De Vries has proposed to associate bud variations with the form of alternative expression of characters shown in accommodations to external conditions (dichogeny). Accommodations and mutations are alike in the general sense that both may be considered as phenomena of alternative expression, but the changes of expression are evidently determined in different ways in the two cases. Bud variations represent definitely determined changes in the expression of the characters, like seminal mutations, but in the condition of dichogeny there is no such definite determination of expression on the part of the plant. Changes of expression continue to be dependent on the external conditions and are readily reversible if the conditions are changed.

The analogy between bud variations and dimorphic branches is much stronger, for both of these changes of expression are determined by the plant instead of depending on changes of environment and after the changes are made they are not readily reversible. It is also to be noted that all the three kinds of changes of expression shown in accommodations, dimorphism, and bud mutations take place during the processes of vegetative growth without any apparent relation to the special organs of the germ cells that have been supposed to control the process of heredity.

For purposes of the study of heredity a very definite distinction is to be made between changes of expression of characters that arise by mutation and those that appear in response to differences of external conditions. The increase in the proportion of simple leaves on cotton plants grown under greenhouse conditions is not the same,

from the standpoint of heredity, as the variation toward simple leaves in an individual plant of Triumph cotton growing under field conditions, as already described on page 17. In the latter case the simple leaves were not induced by the external conditions, or the effect was limited to a single individual that must be supposed to represent an unusually susceptible condition. And in such cases of individual variation the change of expression is much more definite and permanent than when the change is shared by a whole series of plants or by plants of different kinds. The production of simple leaves on fruiting branches of Egyptian cotton in the greenhouse represents a general tendency to reduction of lobes manifested in many kinds of cotton under such conditions.[1]

This distinction does not turn, primarily, on the amount of difference or the extent of the change of expression, but upon the manner and permanence of the change, and the same is true of the changes of expression that constitute the phenomena of dimorphism. The result in both cases is the production of entire leaves; but one case probably represents a definite mutative variation, the other a readily reversible environmental accommodation. Dimorphism and bud mutations may also appear to accomplish the same result, in that two definitely different kinds of branches are produced on the same plant, but in the mutation the change is permanent, whereas the dimorphic changes belong to the series of regular alternations, though maintained by the plants themselves instead of being induced by changes of external conditions.

The substitution of vegetative limbs for fertile branches, as often occurs in the cotton plant, indicates that the external environment is a factor in modifying expression even in distinctly dimorphic characters, though it is not definitely known whether increase of vegetative branches results from the formation of a different kind of buds in the first place or represents a transformation of buds that had a previous tendency to produce fruiting branches. There are indications that both kinds of changes occur, depending on the time when the external conditions are changed. Although the normal course of development follows regular steps it is often influenced profoundly by external conditions, even with respect to characters that are known to be subject also to mutative changes of expression, such as the "cluster" character in cotton. The occurrence of mutative variation has also been found to be influenced by external conditions, mutations being much more numerous in some localities than others, in fields planted with the same selected stock of seed.

[1] Attention has been called by Mr. T. H. Kearney to the fact that similar modifications in oak leaves growing in shaded positions have been pointed out by Brenner in a paper on "Climate and Leaf in the Genus Quercus." Flora, vol. 90, 1902, pp. 114-160.

The two kinds of leaves borne by the two kinds of branches of the cacao tree, for example, are probably much more different than any mutations that have ever been reported. Changes of expression in dimorphic specializations are as great as or greater than in those that give rise to distinct mutative varieties or sports. Dimorphism not only covers at least an equal range of variation, but affects the same kinds of characters as mutative variations. This is shown very definitely in the Upland type of cotton, where cases of okra cottons with dimorphic leaves arise as mutative variations from broad-leaved varieties. The dimorphic condition, at least in such cases, has to be looked upon as a direct product of mutative variation.

Another form of mutation, more common in Upland cotton than mutations to narrow leaves, is the shortening of the internodes of the fruiting branches, as in the so-called "cluster" varieties. This variation also has relation to dimorphism. The shortening of the internodes of the branches, which characterizes the "cluster" varieties, affects only the fruiting form of branches. The vegetative limbs of "cluster" cottons grow quite as long as those of other varieties. The expression of the cluster character is accompanied by the expression of the other characters of the fruiting branches, like the peculiarities that come into expression in only one sex of an animal though capable of transmission through the other sex. Breeders consider that special egg-laying or milk-producing qualities are transmitted by male animals as well as by females.

A further analogy between mutations and dimorphic changes of expression of characters may be found in the fact of coherence. Dimorphic branches do not differ in one character alone. One form of branch differs from another in all of its parts. A whole group of characters clings together, as it were, in expression. In a similar way a mutative change usually involves a large group of characters. The fact of coherence is of practical importance in relation to selection, for it enables mutative variations to be much more easily recognized than if each detail of structure or color were free to change independently. In dimorphism, as well as in Mendelism and mutation, there seems to be a tendency to contrasted expression instead of to blended or graded expression. In other words, these phenomena may be said to be free from the law of regression enunciated by Galton. Contrasted characters not only maintain themselves in expression, but the contrast gains reenforcement by combination with other alternative characters.

When hybrids are made between different species, such as the Upland and Egyptian cottons, it becomes evident that some characters have much more freedom of combination than others. For

example, the purple spot at the base of the petal of the Egyptian cotton may appear in plants which otherwise bring only Upland characters into expression. But the expression of the yellow color of the petals of the Egyptian cotton depends very closely upon the predominance of Egyptian characters in other parts of the plants. Egyptianlike hybrids often have white flowers, but Uplandlike plants with yellow petals are of very rare occurrence and are usually infertile or otherwise abnormal.[1]

RELATION OF DIMORPHISM TO MENDELIAN INHERITANCE.

Dimorphic leaf characters seem to have the same intimate relations with Mendelian inheritance as with the phenomenon of mutation. Indeed, this might be expected from the fact that characters that appear as mutations generally show Mendelian inheritance when crossed with other varieties not affected by the same mutation.

The leaves that follow each other on the same stalk of a plant of Deccan hemp are as definitely different as those that appear on different plants in the second (perjugate) generation of crosses between broad-leaved cottons and narrow-leaved "okra" varieties. A cross of this kind between a narrow-leaved mutation of King and a Texas variety called Edson has been studied by Dr. D. N. Shoemaker and found to represent an ordinary case of Mendelism. In the first or conjugate generation the leaves were quite uniformly intermediate, while the perjugate generation showed all three types of leaves—broad-lobed, narrow-lobed, and lobes of intermediate width like those of the conjugate generation. Deviations from the Mendelian proportions were not greater than could reasonably be ascribed to the effects of cross-fertilization.[2]

Hybrids between another broad-lobed Upland variety of cotton (Keenan) and an "okra" variety (Ratteree's Favorite) have been made by Mr. H. A. Allard in Georgia in connection with his experiments to determine the extent of natural crossing. Photographic illustrations of the leaves of the parent varieties and the conjugate hybrid are shown in Plate V, from some of Mr. Allard's specimens kindly furnished for this purpose. All of the plants of the conjugate generation, 84 in number, had leaves of intermediate form. The behavior of the characters in the perjugate generation has not been reported, but Mr. Allard states that a definite segregation of the parental leaf forms was shown.[3]

[1] Cook, O. F. Suppressed and Intensified Characters in Cotton Hybrids, Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, April, 1909, p. 16; and Hindi Cotton in Egypt, Bulletin 210, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1911, pp. 28-33.

[2] Shoemaker, D. N. A Study of Leaf Characters in Cotton Hybrids. Proceedings of the American Breeders Association, vol. 5, p. 116.

[3] Allard, H. A. Preliminary Observations concerning Natural Crossing in Cotton. American Breeders Magazine, vol. 1, 1910, p. 247.

As the illustrations of the leaves of *Hibiscus cannabinus* have shown, the transition from the entire to the divided leaves is not equally abrupt on all plants, but neither is it usual for the two types represented in a Mendelian progeny to have the contrasted characters equally expressed in all individuals. Narrow-leaved mutations from the broad-leaved varieties of cotton are not all equally narrow leaved, nor do the narrow-leaved members of a series of perjugate hybrids all have leaves with lobes of the same width. The range of variation in the perjugate generation is not only vastly greater in total extent than in the first or conjugate generation, but also seems to be greater among the perjugate plants that represent the narrow-leaved group. It is to be expected, however, that these general differences in the range of expression will also be found to vary in different hybrid combinations, just as there may be differences in the abruptness of the transition from one type of leaves to the other in different varieties.

In progenies raised from the seed of okra-leaved mutations grown in fields of the parent variety and subject to natural crossing, both broad and narrow leaves appeared, rather than leaves of intermediate form. Thus the progeny of a narrow-leaved mutation grown by Dr. Shoemaker at Waco, Tex., in 1906, showed the narrow-lobed type of leaves in only about a quarter of the plants, the remainder appearing to be normal broad-leaved examples of the King variety. The progeny of another okra-leaved mutation of the King, selected at San Antonio, Tex., in 1907 and tested at the same place in 1908, showed 20 plants out of 34 with broad leaves, 13 plants with leaves like the parent mutation, and 1 plant with a more extreme expression of the narrow-lobed tendency, as though another mutative step had been taken.[1]

The second type of dimorphic leaves in cotton, that connected with the dimorphism of the branches, is similarly related with Mendelian inheritance as well as with mutative variation. Branch characters show Mendeloid expression of characters in hybrids, as well as leaf characters. Crosses between cluster and noncluster cottons of the Upland type do not manifest the cluster habit in the conjugate generation, but the cluster character returns to definite expression in the perjugate generation.[2]

The interest of the dimorphic leaves of *Hibiscus cannabinus* in relation to Mendelism is to show that a change of characters quite as extensive and abrupt as those that characterize Mendelian hybrids

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[1] Cook, O. F. Local Adjustment of Cotton Varieties. Bulletin 159, Bureau of Plant Industry, U. S. Dept. of Agriculture, September, 1909.

[2] Cook, O. F. Suppressed and Intensified Characters in Cotton Hybrids. Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, April 7, 1909, pp. 22-23.

may take place in adjoining internodes of the stalk of the same individual plant. There can be no question, in such a case, regarding the separate transmission of the units of the two contrasted characters to different plants. The same plant not only inherits both of the contrasted characters, but brings them both into expression. Such facts may be considered as additional reasons for believing that Mendelian inheritance may be looked upon as a phenomenon of alternative expression of characters. It no longer seems necessary to predicate an alternative transmission of characters, as often assumed in the study of Mendelism.

That the phenomena of Mendelian inheritance are of much significance in the study of heredity need not be questioned, but what the significance may be is still in doubt. It is possible to interpret the facts of Mendelism in at least two very different ways. The mathematical relations of Mendelism are equally well explained, whether ascribed to an alternative transmission of contrasted characters or to alternative expression. Neither transmission nor expression is understood in its essential nature—that is, as a physiological process—but this only makes it the more desirable not to confuse the two processes in attempting to understand them. The importance of distinguishing between expression and transmission is not so obvious, perhaps, as long as investigation is limited to cytological and statistical studies of typical cases of Mendelism, but collateral evidence of other kinds should not be neglected. On this question plants seem to afford better evidence than animals because of their habits of growth by the vegetative multiplication of internodes. Among the internode members of the same plant body there can be no question of differences of transmission, yet definitely contrasted expression remains the rule of development. Not only are there abrupt transitions from one class of internodes to another, but the tendency to contrasted expression is accentuated by dimorphic specializations within the same class.

DIFFERENT TYPES OF DIMORPHIC SPECIALIZATION.

If the internodes of plants be thought of as individuals, the definite differences that exist between the various kinds of internodes of the same plant appear closely analogous to the contrasted characters of the sexes of the higher animals or the several castes that compose the highly organized colonies of bees, ants, and termites.

Species that are composed of two or more sexes, castes, or other distinct kinds of individuals have been called "ropic," a term that denotes a definite tendency to contrasted expression of the characters,

as though the relations that determine the expression of the characters had a definite polarity or repulsion so that the contrasted extremes of a series are manifested rather than the intermediate degrees. Arropic species, on the other hand, are composed of individuals of only one kind, manifesting individual variations, of course, but with no definite tendency to the contrasted forms of expressions shown in sexual or dimorphic characters.[1]

On the basis of these distinctions the cotton plant and its relatives would be reckoned as arropic species, since there is no sexual or other differentiation into distinct types within the species. At the same time it is obviously desirable to have a ready means of designating different forms of structural specialization in plant individuals whether they belong to ropic or to arropic species. Plants that show obvious differences of leaves and flowers are sometimes called heterophyllous or heteranthous, but these terms record merely the fact of diversity, which is often indiscriminate or intergraded, without any definitely established tendency to contrasted expression of characters.

For the designation of cases of definite dimorphic or polymorphic specialization the word "ropic" may be used in combination with other terms to indicate the part affected. Thus the variety of *Hibiscus cannabinus* with the definite dimorphism of the leaves may be described as phylloropic. Cotton, coffee, cacao, and the Central American rubber tree (Castilla) may be described as cladoropic, since they all show definite specialization of two or more forms of branches. Cacao and some varieties of cotton are phylloropic as well as cladoropic, for the two types of vegetative branches are accompanied by definitely different types of leaves, which do not appear in coffee. According to Went[2], Castilla also has two kinds of leaves.

The banana plant and the Indian corn are familiar illustrations of a dimorphic condition of the flowers and may be termed anthoropic, each plant bearing two definitely different kinds of flowers. A more complicated case of specialization of floral differences appears in the Central American rubber tree. The male or staminate individuals bear only one kind of flowers, but the female or pistillate trees bear two kinds, each pistillate inflorescence being subtended by two small staminate inflorescences, not of the same form as those that are found on the purely staminate trees. The species as a whole shows a definite specialization of the sexes, but the female trees may be described as anthoropic because of the two definitely different kinds of flowers.

Many terms are used by students of plant pollination to indicate whether the stamens and pistils are present together in the same

[1] Cook, O. F. Aspects of Kinetic Evolution. Proceedings of the Washington Academy of Sciences, vol. 8, 1907, p. 369.

[2] Went, F. A. F. C. Der Dimorphismus der zweige von Castilloa elastica. Ann. Jardin Botanique Buitenzorg, vol. 14, pp. 1-17.

inflorescences, separated in different flowers of the same plant or on different plants, or whether these organs are alike or different among themselves or ripen at the same or at different times. Yet these terms do not indicate whether the different conditions arise by gradual changes in the expression of the characters or whether the other floral parts are different, as well as the stamens and pistils.

Technical terms can often be avoided in describing the details of structure or behavior in any one species or genus of plants; but they become a practical necessity in the scientific task of comparing and contrasting the behavior of different types of plants. Distinctions need to be carefully drawn so as to recognize as definitely as possible the different kinds of diversity that arise because of the different ways in which the expression of the characters is determined. In some cases it is plain that the external conditions are able to influence the expression of characters during the development of a branch, while in other cases determination of characters of branches and leaves seems to be entirely independent of the environment. It is desirable, therefore, to review briefly the terms that have been applied by morphologists to the structural diversities that most nearly resemble the present cases of dimorphic leaves and branches.

Goebel refers to upright shoots of conifers and similarly specialized trees as orthotropes, and lateral or horizontal shoots as plagiotropes; he also considers that the specialization of the lateral shoots (laterality) is of two kinds, called "labile induction" when the lateral branches are able to assume the functions of uprights, as in Picea, and "stabile induction" when such substitutions can not be made. There is also a distinction to be drawn between two kinds of "stabile induction" of laterality. In some cases the lateral branches are readily able to regenerate upright shoots from lateral buds, as in cotton, while in other cases the lateral branches seem to have no power of replacing the uprights, even from latent buds. This extreme type of specialization shown in coffee, Castilla, and cacao has also been demonstrated by Goebel in *Phyllanthus lathyroides*.[1]

The terms clinomorphy and anisophylly have been used by Wiesner for adaptive modifications of leaf forms connected with differences of position or exposure, but not in relation to dimorphism or contrasted expression of characters as a definite fact of heredity.[2]

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[1] Goebel, K. Einleitung in die Experimentelle Morphologie der Pflanzen, 1908, pp. 86–88.

[2] In Biologie der Pflanzen, Vienna, 1889, Wiesner states: "Many formative processes in plants are induced by the inclination of the organs to the horizon. All phenomena of development induced through position, not explainable through the effects of gravitation alone, should be comprehended under the name clinomorphy. Clinomorphy appears if an organ in the course of its development is so inclined to the horizon that one can distinguish an upper and an under side, and consists in the fact that the upper half takes another form than the lower." (P. 28.)

"Anisophylly is only an inequality of the foliage of the shoot in relation to position and is shown in the under leaves of a shoot becoming larger and heavier than the upper." (P. 33.)

Goebel considers Wiesner's definition of anisophylly too narrow, and would include cases where the leaves on the under side of the shoot are smaller than those on the upper side, as the following statements will show:

By anisophylly we mean that leaves of a different size and of different quality appear on the different sides of plagiotropous shoots; the leaves which stand upon the upper side are usually smaller than those upon the under side, but the converse is also sometimes the case. * * * All the examples have this in common, that the anisophylly occurs exclusively upon plagiotropous shoots and that it is a *character of adaptation* which has an evident relation to the direction of the shoot and especially to its position with regard to light. * * * Herbert Spencer in 1865 first directed attention to the anisophylly of lateral shoots in plants with decussate leaves, as well as to the connection of the anisophylly of higher plants with external factors, especially with light. * * * The term has come to us from Wiesner, although his definition, which is as follows, is too narrow: "I mean by anisophylly that the leaves lying upon the upper side of prone shoots have smaller dimensions than those upon the under side, whilst the lateral ones are intermediate." We know, however, that the leaves on the under side may be smaller, as is the case in the foliose Jungermannieæ and in *Lycopodium complanatum.* [1]

An excellent example of anisophylly is found in the common paper mulberry (Broussonetia), as shown in figure 18. Indeed, Broussonetia may be said to combine two phenomena, for in addition to the distinctly smaller size of the leaves that arise from the upper side of the branch there is a wide range of diversity in the forms of the leaves, which constitutes heterophylly.

Anisophylly is to be considered as a physiological phenomenon, rather than morphological. The inequalities in the size of the leaves are supposed by Wiesner and Goebel to arise by direct accommodation to the position in which they happen to be formed. An accident to a tree that changes the position or exposure of a growing shoot affects the condition of anisophylly by rendering the leaves more or less unequal than they otherwise would have been. Yet the interpretations that have been placed upon anisophylly do not seem to be altogether consistent. In some cases it is considered that the larger size of some of the leaves is connected with better exposure to light, but in Broussonetia it would seem that the light must be supposed to restrict growth, for the smaller leaves are produced from the upper side of the branch. Some writers look upon the small leaves as specially adapted to fit in among the large ones and thus utilize all the surface of exposure. In this view Broussonetia would seem to have overshot the mark. Figure 18 indicates that much

[1] Goebel, K. Organography of Plants, Especially of the Archegoniatæ and Spermaphyta, pt. 1, 1900, pp. 99–100.

Additional cases of anisophylly in tropical plants from the Malay region have been reported by Heinricher in a paper that concludes with a list of several other papers on the subject. (See Heinricher, E. Beitraege zur Kenntnis der Anisophyllie, Annales du Jardin Botanique de Buitenzorg, sup. 3, pt. 2, 1910, pp. 649–664, and pl. 25.

more space is lost between the rows of small leaves and the large ones than between the leaves in the rows.

When a definite dimorphism exists the differences in the leaves or branches are not merely physiological, but morphological. There are two kinds of leaves or of branches, not merely two conditions of the same kind. Anisophylly presupposes only one kind of leaves, but with a wide range of accommodation to external conditions. Inequalities of leaves due to differences of exposure to sunlight may be considered as a weaker form of the same kind of accommodation shown in amphibious plants that produce either an aquatic or an aerial form of foliage, depending on the medium in which they happen to grow.

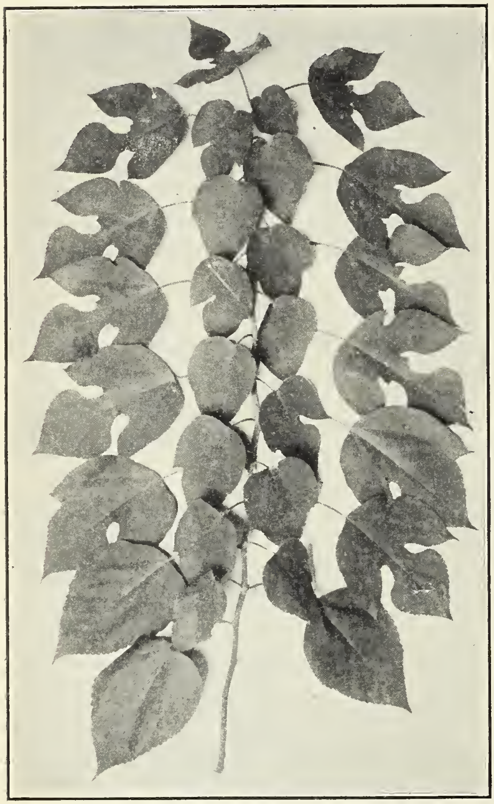

FIG. 18.—Lateral branch of the paper mulberry (Broussonetia), with leaves unequal in size (anisophylly) and diverse in form (heterophylly). (Reduced.)

A term that has a more definite signification from the standpoint of heredity is dichogeny, defined by De Vries as follows:

I mean [by dichogeny] all those cases where the nature of an organ is not yet decided during the early stages of its development, but may yet be determined by external influences. Thus, under normal conditions the runners of the potato plant form at their tips the tubers, but on being exposed to light, or when the main stem has been cut off, they develop into green shoots. * * *

In such cases it is clear that the possibility of developing in either of two different directions is dormant in the young primordia. For this very reason I should like to apply the name *dichogeny* to this phenomenon. And it evidently depends upon external influences what direction is taken. Therefore, a selection must take place from among the available hereditary characters of the species, and this selection may be influenced by artificial interference. For the theory of hereditary characters such experiments are therefore of the highest interest.[1]

[1] De Vries, H. Intracellular Pangenesis (translated from the German by C. Stuart Gager, Chicago), 1910, pp. 15-16.

The phenomena of dimorphism of leaves and branches show a general contrast with the phenomena of dichogeny, since they appear to arise from a definite polarity or determination of expression or nonexpression of certain characters that may not be subject to change through the influence of external conditions. In such cases as the dimorphic branches of coffee, cacao, and the Central American rubber tree (Castilla), it is evident that the nature of the organ is definitely predetermined even in the earliest stages of its development. From a bud in a certain position on the internode only one kind of a branch can arise, while another kind of branch comes quite as regularly from another bud in a different position. The lateral or fruiting branches not only do not transform themselves into vegetative limbs but may even be unable to produce new vegetative shoots from buds. In the cotton plant vegetative shoots can be regenerated from axillary buds of the fruiting branches, but in coffee the fruiting branches can produce only inflorescences or other fruiting branches. The same is true of Castilla, except that the fruiting branches nearly always remain simple. In the cacao tree two kinds of branches are even more definitely specialized in their vegetative characters and functions, though both kinds bear inflorescences.

The word "ropogeny" may serve as a general term to cover such cases of definitely predetermined alternative expression of characters resulting in dimorphism or polymorphism in the branches, leaves, or flowers of the same plant. Ropogeny is to be contrasted with dichogeny, in which the expression of the characters is not definitely determined in the early stages but remains subject to change by environmental influences during the development of the plant.

Dichogeny and ropogeny, used in these senses, are strictly physiological terms. One of the problems in the physiology of reproduction is to understand, as far as possible, how the characters are determined and brought into expression. It is evident from the facts of dichogeny and ropogeny, as well as from the general nature of the processes of development in plants, that expression is differently determined in different plants and even in different parts of the same plant. Not only is there a general distinction to be drawn between transmission and expression of characters, but different forms of alternative expression have to be recognized.

The extent to which expression has been modified by specialization does not appear to have any direct relation to the method of predetermination of the characters. In some cases all gradations may be traced between normal foliage leaves and minute bracts or bud scales, while in other cases there are definite differences between two kinds of large, expanded foliage leaves as shown in the cacao tree and still more strikingly in the related species *Theobroma bicolor*.

These facts may explain why some of the more definite but less striking differences have been overlooked, notwithstanding the attention that has been given to the study of the more reduced and apparently more specialized forms of leaves.

In addition to bud scales and prophylla, special names have been given to the reduced leaves of underground shoots (kataphylls) and to those that subtend flowers or inflorescences (hypsophylls), but these terms seldom, if ever, refer to examples of definite dimorphic differences like those that sometimes exist among true foliage leaves, nor do they serve to distinguish gradual changes of characters from those that are more definite and abrupt.

It is convenient to use a general term (hypophyll) to cover all forms of reduced leaves, since nearly all plants have such leaves, in addition to the true foliage leaves (trophophylls) and the floral leaves (anthophylls). Most hypophylls are formed by the reduction or suppression of the blade and petiole of the leaf, while the sheath or the stipules are retained or enlarged, as in the involucral bracts of the cotton plant. Both the hypophylls and anthophylls may be disregarded in the study of differences among the true foliage leaves.

The terms that have reference to various kinds of differences among the leaves and branches of the same individual plant may be summarized briefly as follows:

Heterophylly, a general term covering all kinds of diversity of leaf forms on the same plant without regard to whether the differences are definite or adaptive.

Clinomorphy, a general term for differences of form arising through oblique or horizontal position.

Laterality, a general name for special characters of lateral branches as distinguished from those of an upright trunk or branches.

Anisophylly, inequality of leaves on upper and lower sides of horizontal or oblique shoots, as in Broussonetia. (See fig. 18.)

Hypophylly, the production of rudimentary or reduced leaves, including prophylls, bud scales, bracts, and other less common conditions, such as the scale leaves above the cotyledons of seedlings of *Persea gratissima* and *Citrus trifoliata* and those near the ends of upright shoots of *Theobroma cacao*.

Phylloropy, production of two or more definitely different kinds of foliage leaves on the same plant, as in the cacao tree and in narrow-leaved varieties of cotton, okra, and *Hibiscus cannabinus*.

Cladoropy, production of two or more definitely different kinds of branches on the same plant, as in cotton, coffee, cacao, and Castilla.

Cladoptosis, the self-pruning habit or spontaneous falling off of specialized temporary branches, as in Populus, Quercus, and Castilla.

Heteroblasty, the production of a distinct type of juvenile foliage as in Eucalyptus, Juniperus, Pinus, Hedera, and Ficus.

Homoblasty, the absence of a distinctive juvenile form of foliage.

Dichogeny, expression of characters not completely determined in early stages, allowing different characters to come into expression as a result of accommodation to different conditions, as in *Solanum tuberosum*, *Ranunculus aquatilis*, etc.

Ropogeny, expression of characters completely determined in the early stages, not subject to modification by differences of external conditions, as in the fruiting branches of coffee, cacao, and Castilla that are unable to regenerate vegetative shoots.

RELATION OF DIMORPHISM TO SEXUAL DIFFERENTIATION OF PLANTS.

Abrupt changes of characters during the development of plants are not limited to these more or less exceptional cases of dimorphic specialization of different kinds of leaves. Even where the leaves are all of one type numerous changes in the expression of characters are required to form the different kinds of floral organs. This requirement of numerous changes of characters during the process of development renders the phenomena of heredity in the higher plants somewhat different from those that are shown in the higher animals, especially when viewed from a physiological standpoint.

The fact that many of the higher plants are self-fertilized is often taken to mean that the principle of sexuality is less important with plants than with animals, but this idea represents only a partial view of the facts. The pollen grains and ovules of plants are not only as definitely differentiated as the sex cells of animals, but they are produced by plant individuals that have a sexual differentiation quite as definite as that of the higher animals.

The plant individual is constituted in a different way from the individual animal, being made up of a large number of internodes or joints often capable of independent existence, if cut apart, or even provided with natural means of separation. In other words, the plant is to be considered as a compound individual or social organization of numerous internode individuals. The stamens and pistils also represent separate members of the series of internodes that make up the compound plant body.

The process of conjugation in plants involves the union of sex cells derived from different individuals, no less than in animals. Self-fertilization simply means that crossing is confined to germ cells produced by members of the same plant colony. The close association of stamens and pistils in the same flower should not be allowed to conceal the fact that these two types of organs are entirely unlike,

not only with respect to their products of pollen grains and ovules, but in other characters. The same freedom of change and contrast of characters apparent in the external visible features may be supposed to exist in internal characteristics of the germ cells.

Plants that produce both stamens and pistils in the same flowers are often described as hermaphrodite, but this normal bisexual condition should not be confused with an abnormal, partial, or intermediate expression of the characters of both sexes in the same individual, as sometimes occurs among sexually differentiated animals. In normally bisexual plants, on the contrary, the characters of both of the sexes are fully expressed in the separate individual members of the colony. Abnormal hermaphroditism, like that of animals, is shown in plants in the rare cases of malformed organs intermediate between stamens and pistils. The abnormal organs heretofore mentioned (p. 22) as intermediate between stamens and petals represent a similar failure of complete change in the expression of contrasted characters, as also occurs in abnormal intermediate forms of branches.

Morphologists may object that the higher animals, as well as the higher plants, have a segmental or metameric structure in the sense that their bodies are made up by the union of structural elements corresponding to the more distinctly segmental bodies of the lower groups of animals. But whatever stress may be laid upon this idea from the standpoint of morphological theories, it is evident that the physiological differences are profound, involving different relations among the primitive segments and different requirements for changes in the expression of the hereditary characters during the processes of development. The processes of heredity, as shown in the formation of the segments, might be described as simultaneous in animals and successive in plants.

The segmental growth of the animal body is determinate at a very early stage, long before the growth in size is completed. In the higher animals the determinate condition is shown most definitely in the female sex, the whole complement of ovules being formed while the animal is still in an embryonic stage of development. In bees and related insects the male sex is more determinate than the female. The plant body, on the other hand, begins with only one or two segments and adds the others gradually during the process of growth. The individual stamen or pistil of a plant is determinate, but most plants can produce an indefinite succession of stamens and pistils as well as of vegetative internodes.

Plants grow chiefly by successive additions of segmental units. The striking fact about the successive additions of new structural units to the plant body is that they are not all alike but are capable

of very abrupt and very extensive changes of characters. After forming, it may be, several kinds of vegetative internodes, the young plant begins suddenly to make floral or reproductive internodes, each kind of internode involving a practically complete change of characters. The idea that plants could produce the slight changes of characters shown in bud mutations has seemed highly improbable to those who have not witnessed such changes, though more extensive changes regularly take place in the development of each plant.

Beginning with the formation of cotyledons or seed leaves, the plumule of the embryo has already provided for an abrupt change to the ordinary form of leaves. Some seedlings show more gradual transitions from the cotyledons to the ordinary leaves, and some have specialized reduced leaves between the cotyledons and the ordinary foliage leaves, as in *Persea gratissima* and *Citrus trifoliata.* The cacao tree often produces similarly reduced scalelike leaves on many internodes near the ends of the upright shoots in addition to two kinds of functional leaves, the ordinary leaves of the upright shoots being different from those of the lateral or whorled branches. Many plants have small entire leaves like those of seedlings at the base of each new shoot, as in the vegetative branches of cotton. In grasses and palms the basal joint of each branch or inflorescence bears a small bladeless sheath, called the prophyllum, similar to the first leaves of seedlings. Pines, junipers, and eucalypts have a distinct juvenile type of foliage in young plants that entirely disappears in adults, though it is recalled to expression when growth is forced from dormant buds after severe cutting back.

Many herbaceous plants have the so-called radical leaves at the base of the stalk much larger and of a very different form from those farther up, a condition that doubtless passes by numerous gradations into the more definite types of dimorphism shown in Hibiscus and Gossypium.

The erect fruiting branches of the English ivy are upright and bushy and have more rounded leaves than the familiar creeping stems. De Vries has shown that the so-called variety arborea represents merely rooted cuttings of the fruiting branches that continue the upright habit of growth. De Vries also found that the seedlings of such a plant were of the usual creeping form, and came to the conclusion that the upright habit was "not inherited." He states:[1]

> In 1893 I sowed the berries of an older plant of this kind, in this case an ivy bush of about 2 meters, and obtained over a thousand seedlings. These still grow in our garden and have made, up till now, exclusively creeping stems and branches. The arborea form is evidently not inherited.

In the same way it might be said that the characters of butterflies are not inherited, since they do not appear in the caterpillar stage

[1] De Vries, H. The Mutation Theory, 1909, vol. 1, p. 44.

of the progeny. Or beards might be considered as not inherited because they are not developed in children. In all such cases there is a temporary latency or postponement in the expression of characters, but no failure of inheritance in the sense of transmission. The adult characters remain latent during the larval or juvenile stages, and the juvenile characters are suppressed in turn during the adult stages. In the development of each individual plant several such changes in the expression of the characters are regularly required for the formation of the different kinds of vegetative and reproductive organs.

In the cotton plant six different forms of leaf organs may be recognized, the cotyledons, the entire or broad-lobed leaves at the base of the stalk, the more divided leaves farther up, the smaller, narrower leaves of the fruiting branches, and the two still more reduced and specialized forms that compose the outer and inner involucres. To form the petals, stamens, and pistils requires three other changes of characters, making nine changes altogether during the course of development of each plant.

The familiarity of the facts makes an adequate appreciation difficult, but if the individuality of the internodes and their method of development, one after another, be recognized, it becomes plain that the changes of characters that take place during the growth of the plant are much more profound than those that are required in the postembryonic development of an animal. The whole complex of characters expressed in one internode individual may give place to the expression of an entirely different complex in the very next internode. Without any opportunity for new conjugations, segregations of characters in different germ cells, or changes in the numbers of chromosomes, one complex of characters after another is called into expression and the previous complex retired to a latent condition.

Failure to effect the full change of expression results in the development of abnormal organs of intermediate form, as in the case of abnormal intermediate branches in the cotton plant. Such branches are usually sterile, or their flower buds are abortive, as in abnormal hybrids or hermaphrodites. The power to complete the various alternations in the expression of the characters determines the possibilities of development in the individual plant, in the same way that the evolutionary progress of a species is determined by evolutionary changes of characters.

The phenomena of alternative expression have been studied largely from the standpoints of environmental modifications and diversities in hybrids. These groups of phenomena are only a small part of the field of alternative expression, which includes also the endless changes of characters that appear during the ordinary processes of

development. Even evolutionary changes appear to depend largely upon the power of alternative expression. After a character has once been acquired transmission seems to be permanent. Characters that are discarded from expression are not dropped from transmission, but may be transmitted in latent or rudimentary form for thousands of generations, as the facts of recapitulation and reversion have shown. The transmission of latent characters should not be considered as a rare or exceptional phenomenon, but as the normal, universal condition.

The internal agencies of the cells, that determine the expression of characters, remain active and capable of profound readjustments during the life history of each individual plant. The changes of characters shown in mutative variations are considered as very important phenomena of heredity, and yet they are far exceeded by the changes that regularly take place during the development of every normal plant. Even the metamorphoses of insects hardly constitute such profound modifications of form and structure as the differences among the internode members of the same plant.

Though the facts of plant development seem to afford little ground for the application of Weismann's idea of a fundamental distinction between the germ plasm and the somatic tissues, a distinction is at least to be made between the processes of inheritance in plants and animals. The unknown internal mechanism that controls the expression of the characters evidently remains in a much more active state during the development of a plant than in the case of an animal. This consideration may help to explain the generally recognized fact that the characters of plants are much more readily modified by changes of environment than those of animals. A recent writer has proposed to explain the greater adaptability of plants and lower animals to changes of environment by framing general laws of diminishing environmental influences in passing from lower to higher groups.[1]

A study of the methods of reproduction and development followed in the various groups may reveal biological facts underlying this generalization. The higher animals, that show the least susceptibility to environmental modification, not only have a more nearly simultaneous determination of the expression of the characters, but their warm-blooded bodies are able to maintain constant temperatures and thus protect themselves against the fluctuations of heat and cold that represent one of the most disturbing factors in the development of plants.

Consideration should also be given to the possibility that the sudden and complete changes of characters involved in the production of the

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[1] Woods, F. A. Laws of Diminishing Environmental Influences. Popular Science Monthly, April, 1910, p. 313.

different kinds of internodes may influence the germ cells and the process of conjugation. The phenomena of sexuality are closely connected with contrasted expressions of characters. Sexuality is primarily a physiological fact, and only secondarily morphological. The physiological value of sexual differentiation must be sought finally in a greater efficiency of the process of conjugation.

In the higher groups of plants and animals there is a double differentiation of sexual characters. The male and female germ cells not only become more and more unlike as the scale of organization is ascended, but sexual inequalities also become more and more developed in the organisms that produce the two kinds of germ cells. Not only the inequalities of the germ cells but also the sexual differentiation of the parent organisms must be supposed to relate in some unknown manner to an increased efficiency of conjugation. Many of the secondary sexual characters of plants and animals are like dimorphic differences in having no direct or obvious use in relation to the external environment, but they may have relation to the internal functions of heredity. Even if considered as mere reflections or anticipations of divergent tendencies of expression embodied in the germ cells, secondary sexual characters would still have physiological significance as showing the fundamental tendency toward alternative expression of characters.

In view of these and other indications that diversity and alternative expression of characters among the members of species have physiological functions in increasing the efficiency of reproduction, it becomes reasonable to consider the possibility that the series of sudden and complete changes in the expression of characters involved in the development of the successive types of internode individuals in plants may also be a factor of heredity. If contrasted parental characters and changes of external conditions affect the vigor of organisms, why may not frequent changes of characters during the process of development be supposed to have a similar advantage? The specialization of two or more different kinds of leaves, branches, or flowers on the same plant may be compared with the alternative inheritance shown in the sexes and castes of animals, and both classes of specialization may have similar relations to the physiology of reproduction. Frequent conjugations between germ cells representing different lines of descent may be rendered less necessary in plants because of the numerous changes of characters that take place during the ordinary processes of growth.

CONCLUSIONS.

A definite dimorphism of the leaves exists in an Egyptian variety of the Deccan hemp (*Hibiscus cannabinus*). The leaves of the upper part of the stalk are deeply three lobed, while those of the lower part

are without lobes. The change from one form of leaves to the other is usually quite abrupt.

The various types of cotton and okra show the same general range of diversities of leaf forms as the Deccan hemp, and some of the varieties have the same tendency to dimorphic expression of the leaf characters. In other words, there is a general parallelism of variation in leaf characters extending through the many species and varieties of cotton, as well as the related genera of plants.

The definite changes of characters involved in passing from one form of leaves or branches to another are analogous to the abrupt transformations that take place in mutative variations. The facts of dimorphism and of bud variation indicate that mutative changes of characters are not necessarily connected with conjugation or with the early stages of sexual reproduction from new germ cells.

Dimorphic differences and mutations show that abrupt changes of characters are to be considered as phenomena of alternative expression. It is obvious that such changes are not determined by alternative transmission, as often alleged for Mendelian segregation of contrasted characters. The same kinds of characters show dimorphic specialization in individual plants and Mendelian segregation in hybrids. Dimorphism and Mendelism may both be interpreted as phenomena of alternative expression.

The general interest of such phenomena is in their relation to the recognition of a fundamental distinction between transmission and expression as a general law or principle of heredity. The facts of heredity and breeding can be better understood if transmission be considered as including the whole ancestral series of characters. Transmission inheritance is a comprehensive process, while expression inheritance is partial and alternative, different characters being expressed in different individuals or in different stages of individual development.

The facts of dimorphism are worthy of being taken into account in breeding, as affording additional varietal characters and as one of the means of recognizing variations from the standard or typical form of a select variety. Dimorphism must also receive attention in the study of the influence of environmental conditions on the expression of characters. In cotton and other tropical crop plants the modification of dimorphic differences represents one of the most serious disturbances of normal heredity induced by external conditions.

DESCRIPTION OF PLATES.

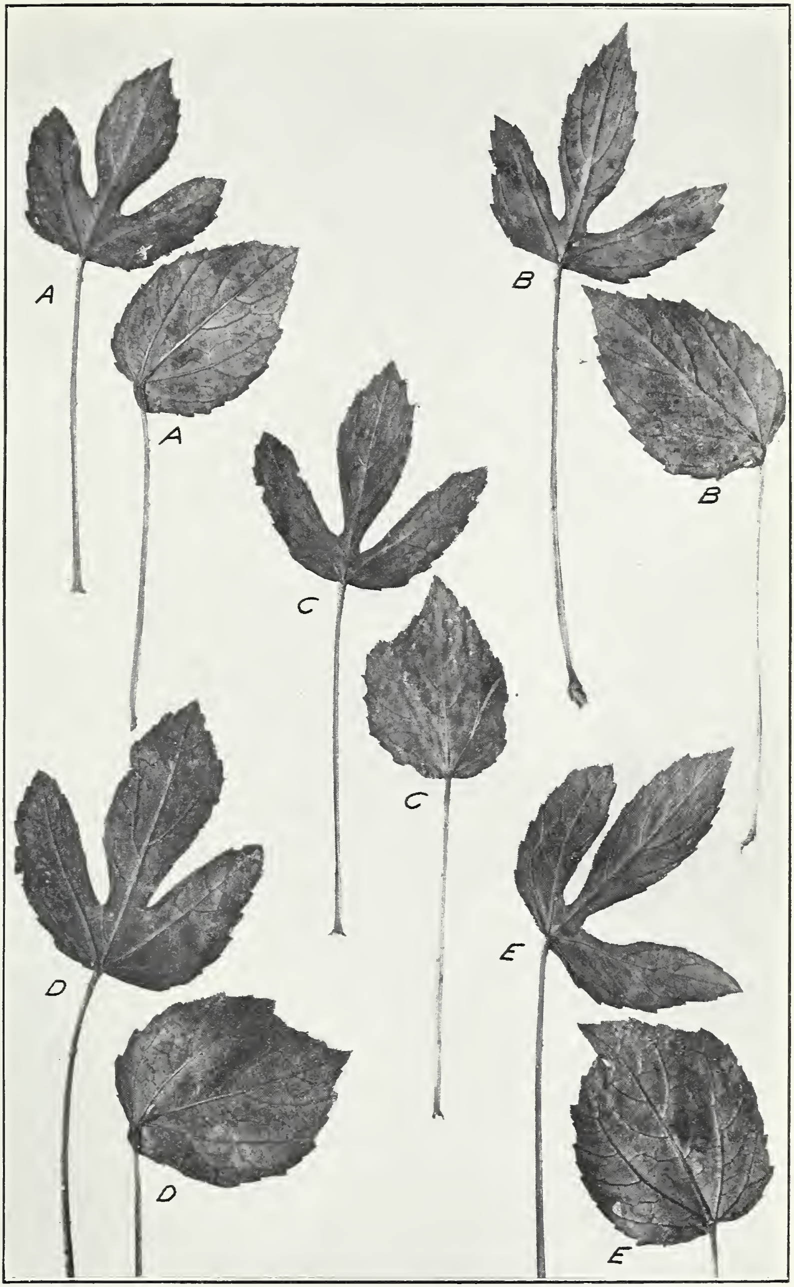
Plate I. Dimorphic leaves from adjacent internodes of five plants (*A*, *B*, *C*, *D*, *E*) of *Hibiscus cannabinus*, two leaves from each plant, the highest of the simple leaves and the lowest of the divided leaves, showing the very abrupt change of form. (Natural size.)

Plate II. Dimorphic leaves from adjacent internodes of four plants (*A*, *B*, *C*, *D*) of *Hibiscus cannabinus*, four leaves from plant *A* and three leaves from each of the others, showing the more gradual changes of characters. The plant leaves shown in this and the preceding plate were collected from plants grown on the borders of cotton fields at Gizeh, Egypt, July, 1910. (Natural size.)

Plate III. End of fruiting branch of Egyptian cotton with normal leaves, stipules, and involucral bracts. Photograph from living plant grown at Sacaton, Ariz., in 1910. (Natural size.)

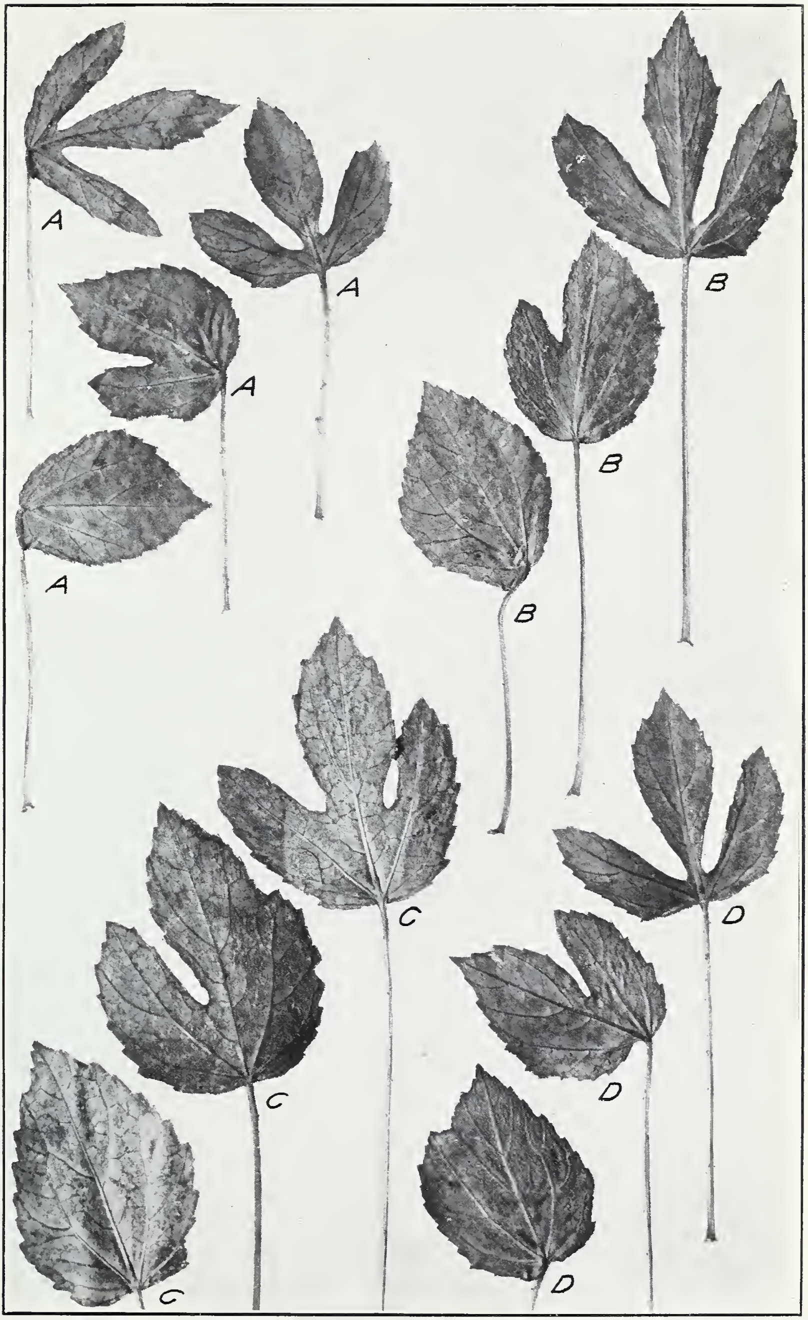
Plate IV. End of fruiting branch of Egyptian cotton with abnormally enlarged stipules and reduced leaf blades, without lateral lobes. Photograph from living plant, Sacaton, Ariz., 1910. (Natural size.)

Plate V. Hybridization of broad-leaved and narrow-leaved varieties of cotton: *A*, Leaf of Keenan variety; *B*, Ratteree's Favorite; *C*, hybrid. Photograph from dried specimens grown by Mr. H. A. Allard at Thompson's Mills, Ga. (Reduced.)



DIMORPHIC LEAVES FROM ADJACENT INTERNODES OF FIVE PLANTS (*A*, *B*, *C*, *D*, AND *E*) OF HIBISCUS CANNABINUS, SHOWING VERY ABRUPT CHANGES OF FORM.

(Natural size.)



DIMORPHIC LEAVES FROM ADJACENT INTERNODES OF FOUR PLANTS (*A*, *B*, *C*, AND *D*) OF HIBISCUS CANNABINUS, SHOWING SOMEWHAT GRADUAL CHANGES OF FORM.

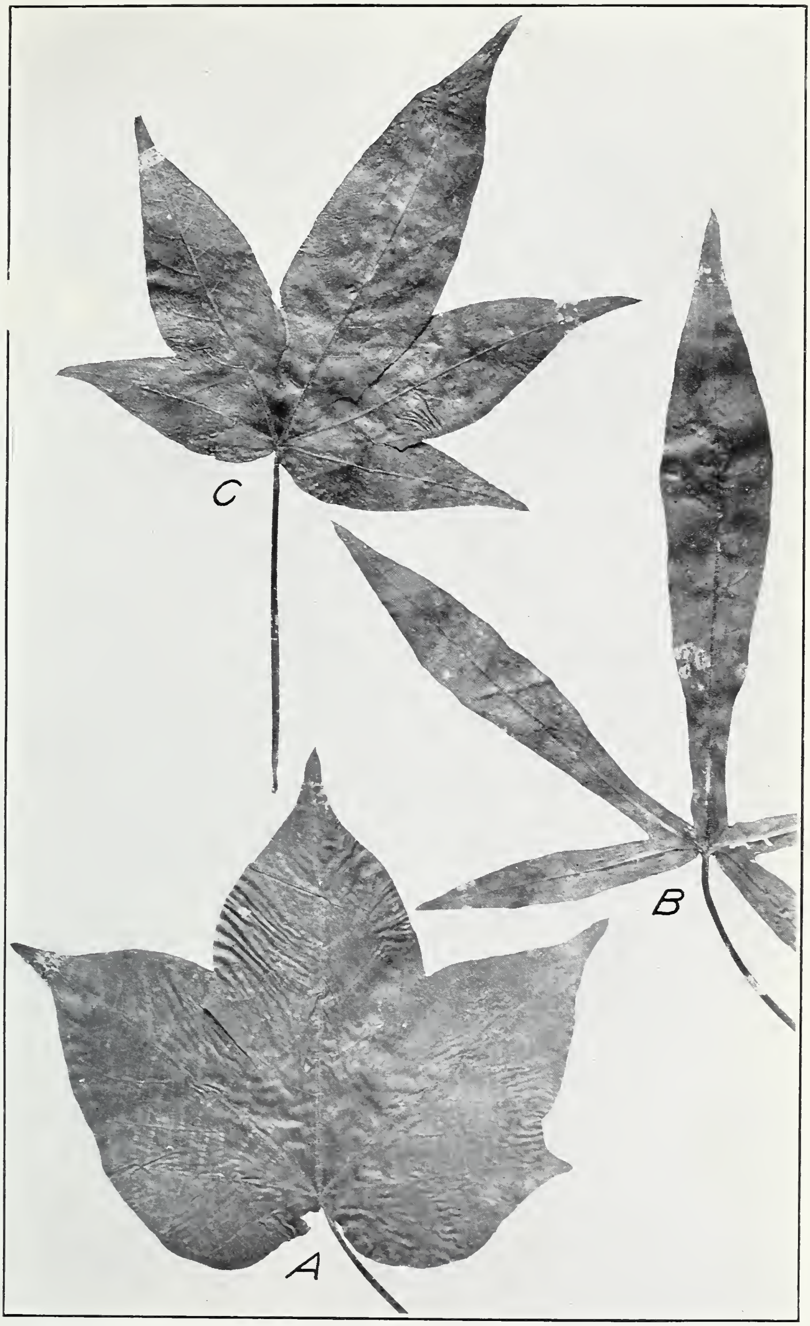
(Natural size.)

END OF FRUITING BRANCH OF EGYPTIAN COTTON WITH NORMAL LEAVES, STIPULES, AND INVOLUCRAL BRACTS.

(Natural size.)

END OF FRUITING BRANCH OF EGYPTIAN COTTON WITH ABNORMALLY ENLARGED STIPULES AND REDUCED LEAF BLADES, WITHOUT LATERAL LOBES.

(Natural size.)



HYBRIDIZATION OF BROAD-LEAVED AND "OKRA" VARIETIES OF COTTON: (A) LEAF OF KEENAN VARIETY, (B) RATTEREE'S FAVORITE, AND (C) HYBRID.

(Reduced.)

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